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THE LIFE HISTORY OF THE RAT LUNG-WORM, *ANGIOSTRONGYLUS CANTONENSIS* (CHEN) (NEMATODA: METASTRONGYLIDAE)

By M. JOSEPHINE MACKERRAS* and DOROTHEA F. SANDARS*†

(*Manuscript received July* 20, 1954)

Summary

Adult *Angiostrongylus cantonensis* live in the pulmonary arteries. Unsegmented ova are discharged into the blood stream, and lodge as emboli in the smaller vessels. First-stage larvae break through into the respiratory tract, migrate up the trachea, and eventually pass out of the body in the faeces.

Slugs (*Agriolimax laevis*) act as intermediate hosts. Two moults occur in the slug, and third-stage larvae appear about the 17th day. The larvae remain within the two cast skins until freed in the stomach of the rat by digestion. They then pass quickly along the small intestine as far as the lower ileum, where they leave the gut and become blood-borne.

They congregate in the central nervous system, and have been found there 17 hr after ingestion. The anterior portion of the cerebrum is the most favoured site, and here the third moult takes place on the sixth or seventh day and the final one between the 11th and 13th days. Young adults emerge on the surface of the brain from the 12th to 14th day, and spend the next 2 weeks in the subarachnoid space. From the 28th to 31st days they migrate to the lungs via the venous system, passing through the right side of the heart to their definitive site in the pulmonary arteries. The prepatent period in the rat usually lies between 42 and 45 days.

I. INTRODUCTION

Lung-worms were discovered by Chen (1935) in wild black and brown rats in Canton, and were named by him *Pulmonema cantonensis*. The only other references found to the occurrence of these parasites in nature are by Yokogawa (1937), who recorded them from wild rats in Formosa, naming them *Haemostrongylus ratti*, and by Matsumoto (1937) from the same locality.

Chen erected the genus *Pulmonema* for this parasite, recognizing, however, that it was close to *Angiostrongylus* Kamenskii 1905. Dougherty (1946) showed that the two were synonymous. The genotype is *Angiostrongylus vasorum* (Baillet 1866) Kamenskii 1905, from the domestic dog. Other species occur in crab-eating dogs, badgers, martens, jerboas, and musk-rats.

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The relevant details concerning the synonymy of the rat lung-worm may be expressed as follows:

ANGIOSTRONGYLUS CANTONENSIS (Chen) Dougherty

Pulmonema cantonensis Chen, 1935.
Haemostrongylus ratti Yokogawa, 1937.

Syntype hosts.—*Rattus norvegicus* (Berkenhout), *R. rattus* (Linné).

Known distribution.—China, Formosa, Queensland.

Dougherty (1946, 1949) placed *Angiostrongylus* in the subfamily Filaroidinae, along with *Aelurostrongylus* Cameron 1927. However, Gerichter (1949) preferred to retain *Aelurostrongylus* in the subfamily Protostrongylinae, where it was originally placed by Cameron, and the arguments for its retention here would apply equally well to *Angiostrongylus*, both genera possessing well-developed bursae.

Our interest in the subject dates from March 1952, when Miss P. E. Lee of this Institute drew our attention to lung-worms in a wild *Rattus norvegicus*, which she was dissecting during a general survey for infective agents. The life history was found to show some remarkable features, a brief account of which has been given elsewhere (Mackerras and Sandars 1954).

II. MATERIALS AND METHODS

We began our investigations by examining wild rats, the majority of which had been caught by dogs belonging to the Brisbane City Council's rat-gang. The lungs and heart were removed from the body, and pinned down in a dissecting dish under 0.4 per cent. saline. The main branches of the pulmonary arteries were then opened up carefully with fine scissors. Adult worms were washed in 0.4 or 0.3 per cent. saline, and killed by dropping into hot 70 per cent. alcohol. They were stored in 70 per cent. alcohol, to which 5 per cent. glycerol was added. Measurements of adults were made in this fluid, and photomicrographs taken after clearing in lactophenol.

The early stages were preserved in a similar way, or mounted in glycerine jelly. Tissues for sectioning and squash preparations of tissue containing early stages were fixed in buffered 10 per cent. formalin, or in Bles' fixative (formalin 7, glacial acetic acid 3, 90 per cent. alcohol 90 parts). They were stained with haematoxylin, or with acetic alum carmine, and mounted in balsam.

These manipulations produced some shrinking and distortion of all stages, the adults being found to lose 10-15 per cent. of their length when dropped into hot 70 per cent. alcohol at a temperature just below its boiling point. Less shrinking occurred when the worms were killed in alcohol warmed only to 40-45°C. However, since many batches of worms had been fixed in hot alcohol, it was necessary to use their measurements in the construction of the growth curve shown in Figure 13.

Young adult males from the surface of the brain were particularly delicate, and liable to rupture at the posterior end. Some were successfully fixed by adding lactophenol drop by drop to the saline containing the worms.

Larvae were measured alive in squash preparations of the tissue containing them. If necessary they were immobilized by heating the slide very gently. Camera lucida drawings of the larvae (Figs. 1-8) were made in this way.

Suspensions of first-stage larvae were obtained from faeces by a modified Baermann technique. Fresh faecal pellets were placed on a layer of muslin and soaked in tap water in a filter funnel fitted with a stop-cock. Lung-worm larvae migrated out of the faeces under these conditions, and after a few hours a rich suspension could be obtained by centrifuging the fluid in the stem of the funnel.

Slugs were kept in glass dressing jars, those measuring 6 in. high by 5 in. in diameter proving satisfactory. The bottom of the jar was covered with a fairly deep layer of smooth river-gravel, which was kept wet. A little leaf-mould was placed on this, and a supply of fresh lettuce leaves given every second day. The jars were covered with muslin. Slugs were handled as little as possible, and were moved from old to new lettuce leaves by means of a wet camel's-hair brush. They were infected by allowing a suspension of larvae to trickle around them from a pipette. The slugs which we used (*Agriolimax laevis*) appear to be attracted to rat faeces, and have been observed eating them. Thus there is the possibility that they may become infected orally, as well as by the penetration of larvae through the body-wall or foot.

III. INFECTION IN WILD RATS

Wild rats were examined from many suburbs around Brisbane, but very few from the city area itself. Nine rats taken in city warehouses were all negative. Of the remainder from the Brisbane district, about one-third came from the northern suburbs, and of these approximately 5 per cent. were infected, one-third from the north-western suburbs, of which 13 per cent. were infected, and one-third from suburbs lying south of the river, of which none were infected. There was one little focus of infection in the suburb of Kelvin Grove (included in the north-western area) where three infected rats were taken from one street. All these suburban areas contain many gardens, where slugs would certainly occur.

We are indebted to Miss C. J. Ross and Miss M. L. Emanuel for the results of examination of wild rats at the Institute's Field Station at Innisfail, north Queensland. These rats were trapped mainly in cane fields.

The results of the examination of rats are set out in Table 1.

As a rule only a few worms were recovered from naturally infected rats, and one sterile infection with a single female worm was observed.

The worms were found in the pulmonary arteries and in their main branches. The lower part of the left lung and the corresponding part of the inferior lobe of the right lung were the sites of election. They usually lay stretched out full-length, and could be seen through the thin wall of the vessel. Sometimes they were loosely coiled in a hypertrophied and dilated part of the vessel.

TABLE 1

INCIDENCE OF LUNG-WORMS IN WILD RATS

Species	Locality	No. Examined	No. Infected	Percentage Infected
R. norvegicus (Berk.)	Brisbane, S. Qld.	158	8	5
R. rattus (L.)	Brisbane, S. Qld.	6	0	0
R. rattus (L.)	Innisfail, N. Qld.	17	2	12
R. assimilis G.	Mt. Nebo, S. Qld.	2	0	0
R. culmorum T. & D.	Benarkin, Central Qld.	18	0	0

IV. MORPHOLOGY

The morphology of the adults has been adequately dealt with by Chen (1935), but a brief re-description is given here for the sake of completeness.

We have found that worms grow very considerably after reaching the lungs, and also that the size attained varies inversely with the density of infection. The following description applies to sexually mature worms taken from the pulmonary arteries.

Male.—Length 15.5-22.0 by 0.25-0.35 mm in maximum breadth. Cuticle smooth, transparent, with faint transverse striae. Head smoothly rounded, no papillae visible in lateral or ventral view (Plate 1, Fig. 1). Mouth without lips. Four pairs of minute, submedian papillae sometimes visible *en face*. Two clearly defined, minute, triangular teeth present at the base of the oral cavity; there appears to be a third tooth, which is difficult to define. Oesophagus 0.29-0.35 mm long by 0.05 mm in maximum breadth at its posterior end. Intestine a wide, thin-walled tube. Excretory pore opens just posterior to the oesophageal-intestinal junction. Spicules subequal, flexible, striated rods. In Chen's type series they measured 1.2 mm in length. In specimens from *Rattus rattus* from Innisfail, north Queensland, they measured 1.1 mm, but in all Brisbane specimens examined they have reached less than half this length, being about 0.49 mm (Plate 1, Figs. 2 and 3). Bursa and rays well developed; ventro-ventral fused to larger ventro-lateral for about two-thirds its own length; laterals arising from a common trunk, latero-ventral being shortest and thickest; dorso-lateral simple; dorso-dorsal short and thick, ending in three small digitations. Gubernaculum absent. One pair of large adanal papillae (Plate 1, Fig. 4).

Female.—Length 18.5-33 by 0.28-0.5 mm in maximum breadth. Cuticle, head, papillae, oesophagus, and intestine as in the male (Plate 2, Fig. 1). In life, the spirally wound, milky-white, uterine tubules and the blood-filled intestine seen through the transparent cuticle form a striking "barber's pole" pattern (Plate 2, Fig. 2). The uterine tubules unite about 2 mm from the posterior end to form a thin-walled vagina. The vulva is a transverse slit. Tail obliquely truncated; anus 0.06 mm and vulva 0.25-0.28 mm from the tip of the tail, which bears a minute terminal projection (Plate 2, Fig. 3).

None of the unfertilized females which we examined had reached maximum size. This retardation of growth was not due to overcrowding. Sterile females from three rats dissected during the tenth week measured from 19 to 25 mm. In one rat, unfertilized females on one side of the chest were 23-25 mm in length, while fertilized females on the opposite side were 30-31 mm. The male: female ratio was usually about 2: 3.

V. THE INFECTION IN THE INTERMEDIATE HOST

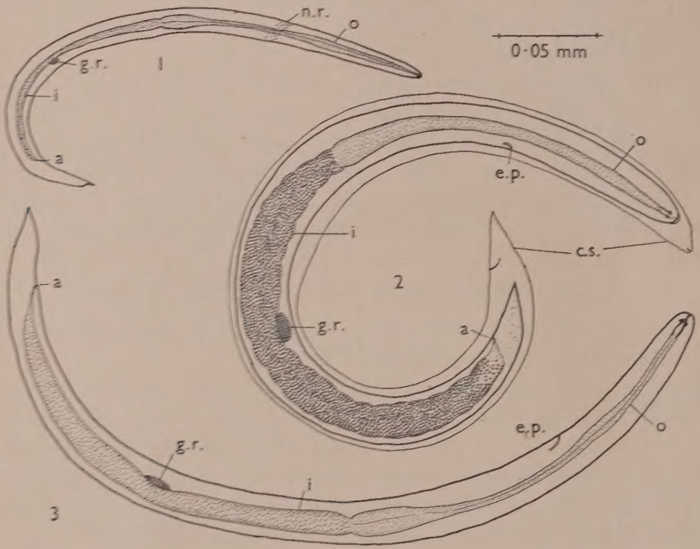
In our preliminary experiments, we used first-stage larvae from the lung or faeces of naturally infected wild rats.

Attempts at direct transmission failed, nor could we infect earthworms, *Pheretima* sp., or cockroaches, *Blattella germanica* (L.), *Leucophaea surinamensis* (L.), and *Periplaneta ignota* Shaw. Garden slugs proved susceptible, and we were able to transmit the parasite to a laboratory rat, which in due course passed large numbers of larvae and provided a steady source of infective material for other experiments. Over 100 laboratory rats were infected in the course of the investigation.

We have found a marked difference in the susceptibility of two common species of garden slugs. *Limax arborum* Bouchard-Chantereaux, a medium-sized, yellowish slug, proved only slightly susceptible, usually yielding a few (1-5) infective larvae per slug. *Agriolimax laevis* (Muller), a small dark slug, on the other hand, proved extremely susceptible, over 200 infective larvae being frequently recovered from one small slug. A large terrestrial slug, *Onchidium* sp., turned out to be a poor host. Larvae invaded the foot normally, and began to develop in large numbers, but relatively few reached the infective stage, the majority becoming surrounded by fibrous tissue and absorbed by the slug. Two rats were nevertheless infected by this species.

(*a*) *First-stage Larva* (*Fig.* 1)

These have been recovered from lung tissue, mucus in the trachea, intestinal contents, and faeces. There was no difference in length between larvae from the lungs and those from the faeces. Length 0.27-0.30 by 0.015-0.016 mm in breadth. There is a short, narrow vestibule leading into a rhabditoid oesophagus, which forms about half the total gut. The oesophagus is slightly swollen anterior to the nerve ring, and has a well-defined, flask-shaped swelling at its posterior end. The nerve ring lies about 0.075 mm from the anterior end. The genital rudiment lies at about the midpoint of the intestine. The anus is about 0.030 mm from the tip of the tail, which is sharply pointed, and bears a distinct though very minute notch on the dorsal surface.



Figs. 1-3.—Stages in the slug. Fig. 1.—First-stage; Fig. 2.—Second-stage; Fig. 3.—Third-stage larva. *a*, Anus; *e.p.*, excretory pore; *g.r.*, genital rudiment; *i*, intestine; *n.r.*, nerve ring; *o*, oesophagus.

First-stage larvae from the lung or faeces are extremely active, but, after penetration into the slug and reaching the body cavity or the muscular layer of the foot, they become quiescent and are characteristically curved in a circle. For several days there is very little increase in length, but the intestinal cells become progressively loaded with food material, so that the larva becomes stouter. From the sixth to the 12th days considerable growth occurs, culminating in the first moult. After this moult the larva does not shed its cast skin.

(*b*) *Second-stage Larva* (*Fig.* 2)

Length 0.420-0.470 by 0.028-0.030 mm in maximum breadth. Minute chitinous, rod-shaped structures appear in the vestibule. The oesophagus has the same general shape and size as in the next stage, but is not nearly so clearly defined. The intestine is composed of large cells loaded with refractile granules. The excretory pore and anus are at first difficult to distinguish, but gradually become clearly defined as the time for the second moult approaches. At first the larva is very sluggish, but it gradually becomes more active, slipping backwards and forwards within its sheath when the dissected foot is squeezed between two slides.

When the metabolism of the stored-up food is complete, usually in about 5 days, the second-stage larva, still enclosed in its first cast skin, moults again, so that it is now encased in two cast skins, or sheaths, which can only be clearly differentiated at the extremities.

The rate of development varied with the temperature. A range from 70 to 79°F proved most favourable, as the worms developed rapidly and the slugs survived well. Higher temperatures speeded up the development of the worms, but there were more deaths among the slugs. At 70-79°F the first moult was observed on the 12th or 13th day and the second about 5 days later. At slightly higher temperatures, 72-83°F, the first moult was observed on the tenth and the second on the 15th day. Larvae were infective as soon as they had moulted for the second time.

(c) *Third-stage Larva* (*Fig.* 3)

Length 0.42-0.49 by 0.025 mm maximum breadth. There are two well-developed chitinous rods with expanded knob-like tips in the vestibule. The rhabditoid oesophagus is about 0.2 mm long. The excretory pore is clearly defined on the ventral surface about 0.09 mm from the mouth. Intermittent pulsations may be seen passing along the canal leading to the pore. The genital rudiment lies about 0.29 mm from the mouth. The anus is about 0.04 mm from the tip of the tail. The intestinal cells have now lost their refractile granules, and the whole larva appears clear by transmitted light.

The third-stage larva remains quiescent within its two sheaths until it is liberated, either naturally by digestion in the rat's stomach, or artificially by dissection. This quiescent period may be prolonged. In a good host the larvae may possibly live as long as the slug, but in a poor host they soon die and are absorbed.

VI. INFECTION IN LABORATORY RATS

(a) *Migration from Gut to Brain*

When an infected slug is swallowed by a rat, the third-stage larvae are set free in the stomach, and some have been found moving actively in its contents 40 min after ingestion. They leave the stomach, move quickly down the small intestine, and have been found in large numbers in the lower ileum about 2 hr after ingestion. They may be found in sections of the wall of this part of the ileum at this period. Between the second and third hours they have been found in the mesentery attached to the lower ileum, once in a small mesenteric vein and once in the tissue. At 4 hr they have been found in blood taken from the right ventricle.

In a rat killed 5½ hr after its first infective feed and 3½ hr after a second one, a few larvae were still present in the stomach, but none were found in the small intestine. In this animal a few were found in a mesenteric lymph gland, three in blood from the portal vein, and three in the inferior vena cava. Blood which oozed from the liver and lungs also contained numerous larvae. No larvae were found impacted in the lung substance, and only one in sections of the liver. This was lying near the periphery of the organ.

At 17 hr, the gut was entirely free from larvae, both contents and gut wall being examined. Two larvae were present in the blood taken from the right ventricle, and numerous larvae were present in blood oozing from the lungs and from the kidneys, though none were detected in blood oozing from either liver or spleen. At this stage, three larvae were found in the cerebrospinal fluid around the cauda equina, and three others were found in squash preparations of the spinal cord, lying either on or in its substance. Twelve larvae were found in the cerebral hemispheres and three in the cerebellum.

At 24 hr, findings were very similar to those obtained at 17 hr, except that larvae were not found in heart blood. They were, however, abundant in blood oozing from the lungs and kidneys, and others had already invaded the spinal cord (four larvae) and brain (three larvae).

It seems evident, then, that the infection is blood-borne for approx. 24 hr at least. Also, since larvae have not been found impacted in the lungs and only once in the liver, they must pass readily through the portal and pulmonary networks, and reach the systemic circulation very rapidly. There is also the possibility that larvae may be able to use anastomoses between abdominal and spinal veins to reach the spinal cord. This may account for what appeared to be an unusual concentration of them in the posterior abdominal wall around the kidneys.

During the blood-borne phase, larvae must be transported passively to all parts of the body, and many may fail to reach the brain. There has constantly been a considerable discrepancy between the number of larvae given and the number recovered from the brain or lungs, suggesting that many are lost during this first migration.

The doses of infective larvae needed to trace the first migration ranged from 500 to nearly 1000. For observations of other stages doses of about 50 to 100 infective larvae were adequate.

In one experiment, infective larvae recovered from slugs by peptic digestion were introduced intraperitoneally into two rats. Both animals began to pass first-stage larvae in their faeces after the normal prepatent period, showing that the introduced larvae had been able to reach the brain and eventually the lungs in the usual time.

(*b*) *Growth in the Brain*

When the larvae reach the brain, they tend to congregate in the anterior part of each cerebral hemisphere, particularly in the extreme tip. On one occasion 25 larvae were found in a thin slice of tissue which included the anterior pole of one hemisphere. They move in the grey matter without causing obvious haemorrhage or reaction.

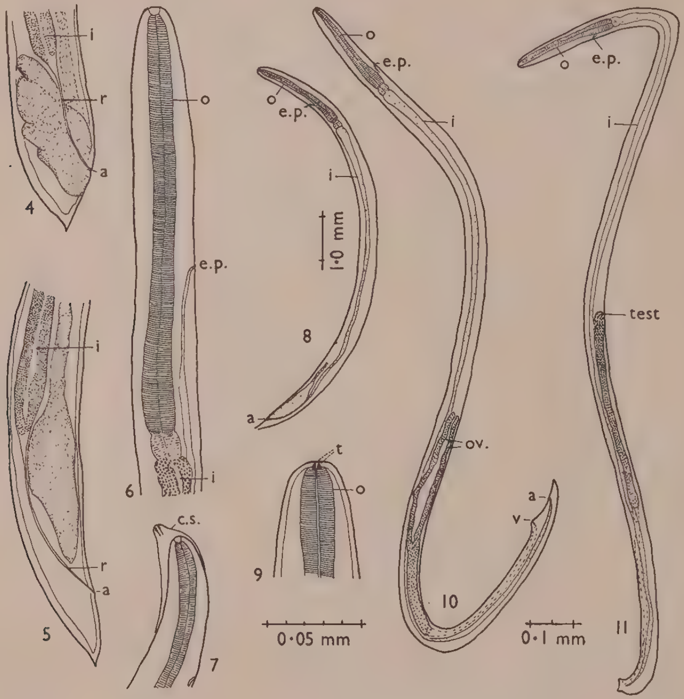
The third-stage larva becomes sluggish, and its intestinal cells become loaded with food material. On the sixth or seventh day after ingestion, the third moult occurs. In a rat dissected on the sixth day, most of the larvae were still in the third stage, but a few were seen to be moulting. On the seventh day, the majority had already moulted and escaped from their cast skins, but one was seen still dragging its sheath (Plate 3, Fig. 1).

(i) *Fourth-stage Larva* (Figs. 4-8).—Length 0.85-1.0 by 0.035-0.04 mm in breadth. Oesophagus resembles that of the succeeding stage in conformation and is 0.24 mm long. The chitinous rods with knob-like ends, which are characteristic of the third-stage larva, are lost in this moult (Figs. 6, 7) and the fourth-stage larva has a simple vestibule without any specialized structures. The sexes can be distinguished at this stage by the shape of the tail region. In both sexes the tip is pointed, but in the male a swelling, which is due to the developing accessory organs, appears just anterior to the anus and dorsal to the rectum (Fig. 4). In the female the tail is not so swollen, but there is a definite mass lying ventral to the rectum and pushing it up towards the dorsal body-wall (Fig. 5). The gonads begin to grow forward rapidly in this stage, the proliferating anterior portion staining deeply with basic dyes.

In serial sections of the brains of rats killed during the first week, the only lesions seen have been accumulations of small round cells and phagocytes. These were particularly numerous in the anterior pole of the cerebrum on the seventh day, but some were seen on the sixth day. A few surrounded the remains of dead worms, but most were definitely around cast skins (Plate 3, Fig. 2), which seemed to act as foreign bodies, whereas living worms caused no apparent reaction in the grey matter (Plate 3, Figs. 3 and 4).

From the ninth day onward, and possibly earlier, some larvae may be found on the surface of the cerebrum. The majority, however, remain within the grey matter until the final moult takes place. This happens between the 11th and 13th days. The young adults leave their cast skins, and gradually make their way to the surface of the cerebrum.

(ii) *Young Adults* (*Figs.* 10 *and* 11).—Length of the newly moulted adults approximately 2 mm by 0.05-0.07 mm maximum diameter. Oesophagus 0.25 mm long. The mouth possesses two (possibly three) well-defined triangular teeth (Fig. 9). The male gonad grows forward as a single cord of cells, whilst that of the female splits into two cords (Figs. 10, 11). The male possesses a tiny, delicate bursa, and there are indications of the developing spicules. The female tail is pointed, and the vulva is clearly marked. There is not much difference in the size of the worms at this stage, though the females tend to be a little longer and thicker.



Figs. 4-11.—Stages in the rat. Figs. 4-8.—Fourth-stage larvae, seventh day. Figs. 10 and 11.—Adults, 13th day. Fig. 4.—Posterior end (male). Fig. 5.—Posterior end (female). Fig. 6.—Anterior end. Fig. 7.—Third moult. Fig. 8.—Whole larva (female). Fig. 9.—Head of young adult, showing teeth. Fig. 10.—Female, and Fig. 11.—Male, in squash preparations of cerebrum. *a*, Anus; *e.p.*, excretory pore; *i*, intestine; *o*, oesophagus; *ov.*, ovaries; *r*, rectum; *t*, teeth; *test.*, testis; *v*, vulva. (Figs. 4, 5, 6, 7, and 9 are to the same scale.)

The meninges react to the invasion by the worms by dilation of the vessels, leucocytic infiltration, and some proliferation of the pia-arachnoid membranes (Plate 3, Fig. 4). This is particularly marked at the anterior pole, and here glial scars are more numerous than elsewhere.

The young adults continue to wander over the surface of the cerebrum until the 28th day or a little later. In light infections they are usually confined to the upper surface of the cerebrum, but in heavy infections may be found on all parts of the brain. In a rat killed on the 29th day, a worm was found in sections in a lateral ventricle. It was surrounded by leucocytes. By this time, the meninges have become considerably thickened and the vessels widely dilated and engorged (Plate 4, Figs. 1 and 2). In one animal, which had been very heavily infected, the brain was not only intensely congested, but presented two necrotic areas on the upper surface of the cerebrum, surrounding the remnants of dead worms (Plate 4, Fig. 3). In another heavily infected animal killed on the 28th day, some of the veins in the pia-arachnoid were thrombosed, these lesions being most marked near the anterior pole of the cerebrum.

In light or moderate infections, the rats show no evidence of cerebral derangement at any stage. However, of two pregnant females given heavy doses for four successive days, one was noticed to be circling the cage on the fifth day, and both animals ate all their young after parturition a day or two later, an action which is generally an indication of some disturbance at that time.

(*c*) *Migration from the Brain to the Lungs*

The young adults in the subarachnoid space are separated from the interior of the veins by walls which are only one cell thick. At this stage the females are about 12 mm and the males 11 mm long. The anterior tip is about 0.06 mm wide. The diameter of the worm gradually increases to a maximum of 0.22 mm in the female and 0.16 mm in the male (these measurements being made from preserved material). They can apparently force their way into turgid veins, aided probably by the teeth in the base of the mouth, and pass out of the skull in the venous blood stream. One was seen in sections in a vein at the base of the brain in an animal killed on the 29th day (Plate 4, Fig. 2). Worms have been recovered from the external jugular vein (which drains the cranial cavity in the rat) in two animals killed on the 29th day, from the left superior vena cava twice, and from the right ventricle on seven occasions between the 29th and 32nd days.

No worms have been found on the brain after the 31st day, though they have been found in the heart on the 32nd day, so that migration apparently is not always complete by that day. Young adults have occasionally been found in the lungs as early as the 28th day, so that for 4 days, the 28th to the 31st, the infection may be divided between brain and lungs.

The meningeal reaction gradually subsides after the worms have left the brain. At 39 days the meninges were still thicker than normal, and there were many cells loaded with blood pigment, while within the cerebrum phagocytosis of some dead worms was seen. By the seventh week the surface of the brain appears normal to the naked eye.

(*d*) *Development in the Lungs*

When the young adults reach their definitive site in the pulmonary arteries, their intestines soon become distended with imbibed blood (Plate

2, Figs. 1, 2, and 3; Plate 5, Figs. 1 and 2). Growth, particularly of the gonads, is rapid. Females grow faster than males, and the ovarian tubules soon become spirally coiled.

The exact period necessary for the maturation of the gonads is not known, but some observations indicate that about a week or 10 days is required. Oviposition had not begun in one animal killed on the 33rd day, nor in another on the 36th day. In another rat killed on the 39th day the lung parenchyma was studded with ova in the early stages of segmentation, but no larvae were present. By the 42nd day the lung contained many fully developed larvae. Fertilization probably takes place soon after the worms reach the lungs, and oviposition begins early in the sixth week.

The ova are unsegmented when shed into the blood stream, and are carried by it into the smaller vessels in the lung substance, where they lodge as emboli. Development to first-stage larvae occurs here, and all stages of segmentation may be found adjacent to one another in sections of the lung (Plate 5, Fig. 4). The first-stage larvae break through into the respiratory tract, where they have been seen in sections of alveoli and bronchioles and in smears of tracheal mucus, so it is apparent that they pass up the trachea and are swallowed.

Larvae usually appeared in the faeces between the 42nd and 45th days, but on a few occasions were not detected until the 48th day. As worms leave the brain over a 4- or 5-day period, some variation in the prepatent period (i.e. the period between infection and first-stage larvae appearing in the faeces) is to be expected.

VII. The Pulmonary Infection

(*a*) *Effect on the Rat*

Experimentally infected white rats cough and sneeze at times, and their breathing is often wheezy, but they usually grow fairly well, mate, and produce young. Nevertheless, there were several deaths among the experimental animals, all of which were about 6 weeks old at the time of infection. Several other infected animals were thin and unthrifty looking.

Eight deaths in all occurred, between the 48th and 299th days, among 20 rats which formed our infected stock. Two of these animals were decomposed when found, but the other six were autopsied. Worms were found in each animal, either within the right ventricle, or tightly packed in the pulmonary orifice and projecting into the lumen of the ventricle. At first this was thought to be due to movement of the worms after the death of the host, but one young rat was actually seen immediately before death. It was cyanosed and gasping for breath. It was opened up immediately after death, and nine female worms were found to be completely blocking the pulmonary orifice. It seems likely, then, that the blocking of the common pulmonary artery by worms retreating from the lungs may be a frequent cause of death.

Many of the experimental animals, which were killed at various stages, were found to have very little healthy lung tissue, and it seems unlikely that they could have survived long under natural conditions.

(*b*) *Lesions in the Lungs*

The earliest lesion in the lungs was seen on the 28th day after infection, and the first after the invasion of the lungs by the worms. There was oedema around the arterioles and bronchioles, and a leucocytic infiltration which was mainly eosinophilic. Similar lesions were seen on the 29th day (Plate 6, Fig. 1). In one animal, killed on the 33rd day after infection and before any ova were deposited in the tissues, there was consolidation of the lower pole of the left lung and the corresponding part of the right inferior lobe. The peri-arterial tissue was crowded with eosinophils (Plate 6, Figs. 2 and 3). In another animal killed on the 36th day, still before egg-laying began, the reaction was similar but less extensive. There is thus evidence of considerable individual variation in the reaction.

When egg-laying is established, the lung parenchyma soon becomes filled with developing ova, and the lungs increase steadily in size and weight. In a rat killed during the ninth week, i.e. only about a month after the invasion of the lungs, these organs were already 10 times their normal weight.

The fully developed infection is obvious externally to the naked eye. The infected lobe is swollen, with a mottled appearance (Plate 2, Fig. 4), the pleural covering is tense, and the tissue firm to the touch. There is often a sharp line of demarcation between normal and infected tissue, like an infarct. On section, the cut surface appears solid, pale, and friable, and may be practically airless. Frequently there are normal alveoli between masses of developing larvae, and no sign of reaction around them (Plate 5, Figs. 3 and 4). On the other hand, the intervening tissue may be emphysematous, or there may be exudation into the alveoli and bronchioles, "heart-failure" cells in the alveoli, and an infiltration of leucocytes into the surrounding tissue.

The arteries containing worms become hypertrophied to accommodate their increasing bulk, the female worms, for instance, growing from 12 mm long by 0.2 mm in breadth to 30 by 0.5 mm. To the naked eye, the surface of the intima may be stained brown with altered blood or covered with whitish plaques. In section, the walls are hypertrophied, and the intima is sometimes greatly proliferated and thrown into folds. The small vessels may be obliterated by pressure and the blood supply of whole blocks of tissue interfered with, causing death and disintegration of the cells. The lung substance is gradually replaced by fibrous tissue.

In animals in which the infection had been present for 6 months or more, the changes in the lungs were more advanced than in any of the naturally infected rats we had examined. There was a marked increase in size and weight of the lungs, so that they sometimes constituted 10 per cent. of the total body weight (normal about 0.5 per cent.). In two rats dying at 10 months, the lower poles of the left lung and of the inferior lobe of the right were extremely hard, of almost cartilaginous consistency. One of these animals had a relatively large abscess involving the whole of the upper pole of the left lung. There were pleural adhesions. On section, the normal architecture of the lung was found to have been completely destroyed, the organ consisting of fibrous tissue and necrotic areas. Lung-worm larvae were still present, many completely imprisoned in fibrous tissue (Plate 6, Fig. 4). Nevertheless, these rats were still excreting normal larvae, since the lesions in some parts of the lungs were not so far advanced—the post-caval lobe of one animal, for instance, presenting the appearance of a more recent lesion, suggesting that worms may have retreated from another lobe and entered the post-caval branch of the artery fairly recently.

VIII. Observations on the Growth Rate

The life of these worms consists of alternating periods of intense activity and quiescence, and alternating periods of rapid growth and periods when growth is at a standstill. There are several periods of considerable hazard to the worm, notably during the first and third stages.

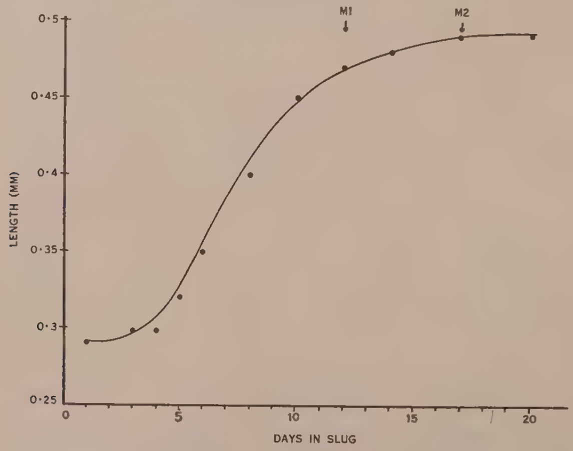


Fig. 12.—Growth curve of larval *An. cantonensis* in the slug *Agriolimax laevis*. *M*1, first moult; *M*2, second moult.

The first-stage larva is extremely active until it penetrates into a slug, when it becomes quiescent, and food material accumulates in the gut. At first there is relatively little change in length, but a considerable increase in girth. Just before the first moult a fairly rapid growth occurs, but once this moult has taken place there is again relatively little change in length. Metabolism of the food already stored goes on during the second stage, which is a wholly quiescent one. The third-stage larva, which appears after the second moult, differs appreciably in appearance from the preceding stage, being definitely slimmer and more transparent. This stage is quiescent in the slug, and may last a long time—perhaps as long as the slug lives, provided it is a favourable host.

Once liberated in the rat's stomach, the third-stage larva becomes extremely active, coiling and uncoiling and thrusting forwards in a purposeful manner. When, however, it reaches the grey matter of the cerebrum, it becomes sluggish, and again this sluggish period is one of steady absorption of nutriment, comparable with the growth of the first-stage larva in the slug, and producing much the same appearance, as the intestinal cells once more become loaded with refractile material. However, the comparison soon breaks down, for, after the third moult, the fourth-stage larva escapes at once from its cast skin, continues to absorb nourishment, and grows relatively rapidly. This stage is short and fairly quiet, the whole of it usually being spent within the grey matter.

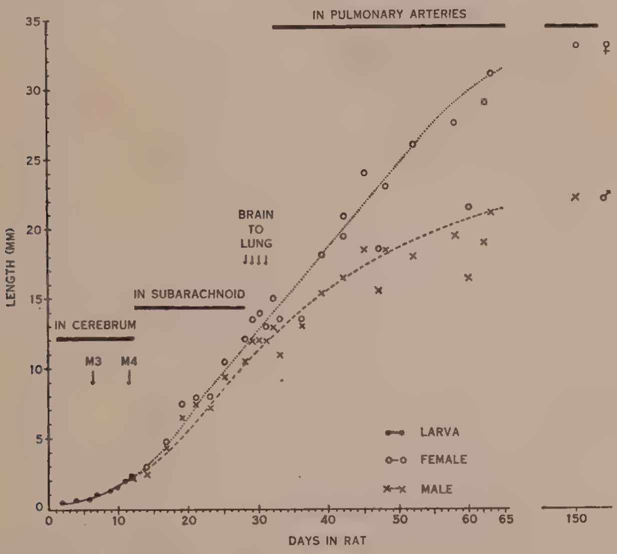


Fig. 13.—Growth curve of *An. cantonensis* in the rat. *M*3, third moult; *M*4, fourth moult.

After the fourth (and final) moult, the young adults proceed to the subarachnoid space and grow steadily. On the 28th day or a little later, some stimulus causes them to force their way into the venous system, and they are carried in the blood stream through the right side of the heart.

Once settled in the pulmonary arteries, there is a rapid development of the gonads. Worms almost reach maximum size by the ninth week, but, if many are present, they may never attain it. Females which are unfertilized may also fail to reach maximum size.

It is noteworthy that the oesophagus grows very little in relation to the rest of the body. Thus, in the first-stage larva the oesophagus forms nearly 50 per cent. of the gut, in the third-stage it forms about 40 per cent., in the fourth-stage 25 per cent., and in the young adults about 12 per cent. of the whole. In sexually mature adults it forms less than 2 per cent. of the gut.

The growth of the worms is shown graphically in Figures 12 and 13, using the maximum recorded length at each stage as an indicator of what happens under favourable conditions.

IX. THE COURSE OF INFECTION IN OTHER RODENTS

(*a*) *White Mice*

When white mice were fed infective slug material, the results depended very largely on the size of the dose. When this was small (say 20-30 larvae), the mouse showed no ill effects at all, but with increasing dosage the likelihood of severe nervous symptoms developing also increased. Out of five mice fed material containing 70-100 infective larvae, all but one showed evidence of cerebral irritation, and four died, or were killed when moribund, between the second and fifth days. The fifth animal died on the 18th day.

The first signs of illness were incoordination of gait, disinclination to move, and bleariness and closure of the eyes. When handled, twitching of one or other limb sometimes occurred. When forced to move, the animal would turn in a tight circle. Gradually it became comatose and died.

On post-mortem examination, no macroscopic lesions were found in the brain, except a small superficial haemorrhage in the parietal region of one mouse. Larvae were not localized in the anterior parts of the cerebral hemispheres, as in the rat, but were found in serial sections scattered throughout the whole brain, including the cerebellum and brain stem, and also in the spinal cord.

Histologically no haemorrhages were seen, and very little sign of reaction to living lung-worms. Dead worms in various stages of disintegration and absorption were seen surrounded by dense masses of small round cells and phagocytes.

As there were no gross lesions in the brain to account for the death of the mice, it was thought possible that a virus might have been carried into the brain by the larvae migrating from the gut. In order to test this hypothesis, a mouse was sacrificed on the fifth day when moribund, and its brain was passaged to other mice by Mr. J. G. Carley of this Institute.

However, no virus was demonstrated, and it was concluded that the symptoms must be due to damage to nerve cells caused by larvae wandering in the brain, particularly in the cerebellum, brain stem, and spinal cord.

Mice which survived for the first 5 days usually showed no signs of infection at later stages. Living worms were recovered from within the grey matter of the cerebrum or from the cerebellum in three out of four mice autopsied during the fourth week, and one was seen in sections in the subarachnoid space between the cerebellar lobules on the 19th day. These worms had reached the adult state and had grown considerably, those from one animal measuring almost 5 mm long. This is in marked contrast to what occurs in the normal host, in which the young adults leave the grey matter by the end of the second week, when they are only about 2 mm long. In one of these animals, a well-grown but dead worm was found surrounded by phagocytes (Plate 4, Fig. 4).

No lung infection was found in 10 mice kept for 6-9 weeks after ingestion of infected slugs. However, in three of these, in which the brain was also examined, remains of dead worms were found in the cerebrum.

Although mice are closely related to rats, it appears that *An. cantonensis* cannot come to maturity in them. In fact, the two organisms are ill adapted to each other, as the worm may kill the mouse by its wanderings in the brain, and the mouse in turn certainly destroys the worm.

(*b*) *Guinea Pigs*

These animals suffered little or no damage from the wanderings of the lung-worm larvae. Doses of 100-200 infective larvae failed to produce any signs of cerebral derangement. However, five animals killed between the seventh and 19th days had either living or dead worms in the brain. Two living larvae, found in the cerebrum on the 12th day, were 0.95 mm long and had reached the fourth stage, but, in another animal killed on the 17th day, only two third-stage larvae were found alive, and these had not grown at all. There was no macroscopic pathology, but the microscopic lesions were similar to those seen in the mouse.

The lungs of four guinea pigs kept for 5-8 weeks after ingestion of infected material were free from lung-worms.

It appears, then, that the guinea pig is a still less favourable host than the mouse. Even after big doses, only a few larvae reach the brain, and, of those which succeed in doing so, the majority soon die. A few may survive for 2 weeks or more without growing, some may grow a little and even moult to the fourth stage, but none manage to reach the lungs.

X. DISCUSSION

The complete life histories of several species of metastrongylid lungworms have been worked out, while many others are partially known. Kauzal (1933) studied *Dictyocaulus filaria* (Rud.), observing two moults in tap water, and one in the sheep. After ingestion, the third-stage larvae congregated in the mesenteric lymph glands before they migrated to the lungs, where the final moult took place.

Schwartz and Alicata (1934) followed the development of *Metastrongylus elongatus* (Dujardin) in earthworms and in pigs. Two moults occurred in the earthworm, and two in the pig, either in the mesenteric lymph glands or in the lungs.

Hobmaier and Hobmaier (1935) studied the cat lung-worm *Aelurostrongylus abstrusus* (Railliet). They found that the intermediate host was a mollusc, and that the infective larvae left the gut of the cat in the oesophagus or stomach, appearing very shortly afterwards in the lungs, where the final moult occurred. Gerichter (1949) studied the same parasite, finding a number of Palestinian molluscs to be susceptible. Infective larvae were obtained after 18 days in the mollusc at optimum temperature. Kittens were successfully infected, first-stage larvae appearing in their faeces on the 39th day after ingestion of infected molluscs.

These periods are very similar to those observed by us under optimum conditions, namely 17 days in the slug and 42-45 days in the rat, giving an egg-to-egg cycle of between 8 and 9 weeks for each parasite. However, *Ael. abstrusus* differs in many respects from *An. cantonensis*, being much smaller, and living in the lung parenchyma, not in the vessels (Gerichter 1949). The similarity in the prepatent periods may be quite coincidental. The similarity of the early stages in the slug is, however, very striking.

Gerichter (1951) also studied the life history of the goat lung-worm, *Cystocaulus ocreatus* (Railliet and Henry). He obtained infective larvae from many molluscs on the 18th or 19th day, and successfully infected a suckling kid, which passed first-stage larvae in its faeces after 42 days, periods almost identical with those observed for *An. cantonensis*.

From the literature, then, we had no indication that the cycle in the rat would include such curious migrations as we have found to occur regularly, unless an observation recorded by Gerichter is an indication that *Cystocaulus ocreatus* may have a period of development in another part of the body. A second suckling kid was infected in the experiment quoted above, but it died of an intercurrent infection during the third week. No worms were found in its lungs (which would be the finding in a rat at that stage), though its companion was later found to be heavily infected.

Nematodes, however, have for long attracted attention by their occurrence within the central nervous system of various animals, and the term "cerebrospinal nematodiasis" has been used by Innes and Shoho (1952) for this condition.

In many instances, the worms found in these odd situations are almost certainly in the wrong host. For example, an epizootic cerebrospinal nematodiasis occurs at times in goats in Japan, and has been proved experimentally to be due to the larvae of a cattle filariid, *Setaria digitata*

(Linstow 1906), transmitted accidentally to goats by mosquitoes (Ishii *et al.* 1953). Sprent (1954*a*, 1954*b*) has reviewed the whole subject, and has contributed largely to an understanding of the migrations of various larval ascarids in the brains of mice, which were in some cases foreign hosts and in others normal intermediate hosts.

As well as larval worms, adults have also been recovered from the central nervous system, and have sometimes been associated with paralysis or death of the affected animal. Thus, Kennedy, Whitlock, and Roberts (1952) described a paralytic disease of sheep in America caused by the presence of a filariid worm, *Neurofilaria cornellensis* Whitlock, in the spinal cord of the affected animal. Similarly, Burg, Baudet, and Verwey (1953) reported fatal intracranial haemorrhage in a deer, due to mature specimens of a metastrongyle, provisionally diagnosed as *Protostrongyloides cervi*, in the subarachnoid space.

Perhaps the most pertinent observation is that of Wolffhügel (1934), who described a common paralytic disease of domestic cats in Chile, which was caused by a metastrongylid worm, *Gurltia paralysans* Wolffhügel, lodged in the dilated and thrombosed veins around the lumbar cord. Adult male and female worms and developing ova were found, but no larvae. The condition of the lungs was not mentioned. It is possible that this parasite normally inhabits the lungs of one of the native felines of the country, and that in domestic cats it fails to complete its cycle, although able to reach sexual maturity within the veins of the spinal cord.

There is therefore ample evidence that many parasitic nematodes have a strong propensity for wandering in nervous tissue. The discovery that such a migration is an essential part of the life cycle of at least one metastrongylid gives some point to such a tendency.

The behaviour of the rat lung-worm in other rodents was particularly instructive. Invasion of the central nervous system occurred in mice and guinea pigs, but it was only in the former, more closely related host that development proceeded to the adult state. Then, instead of migrating to the surface of the brain, the young worms remained within its substance, or reached the meninges in an unusual place, growing larger and therefore more capable of inflicting damage. The lethal effect of large numbers of small larvae wandering in the brain of mice is also noteworthy.

It is hardly likely that *An. cantonensis* is unique in having a phase in nervous tissue, and it may well be that some other metastrongylids, and even some filariids, require a period of development in nervous tissue before proceeding to their definitive site. This period is a silent one in the natural host, but may cause symptoms in an abnormal host. It is also conceivable that a phenomenon of this kind may explain some obscure cerebral pathology in man. Beautyman and Woolf (1951) found a larval *Ascaris* in the brain of a child dying of poliomyelitis, and they made the additional suggestion that viruses might be introduced into the central nervous system by larval nematodes travelling from the gut. The search for these small worms in large quantities of brain tissue is by no means easy, and it is not surprising that they have so rarely been found. A fresh investigation, using modern techniques, would be highly desirable.

XI. Acknowledgments

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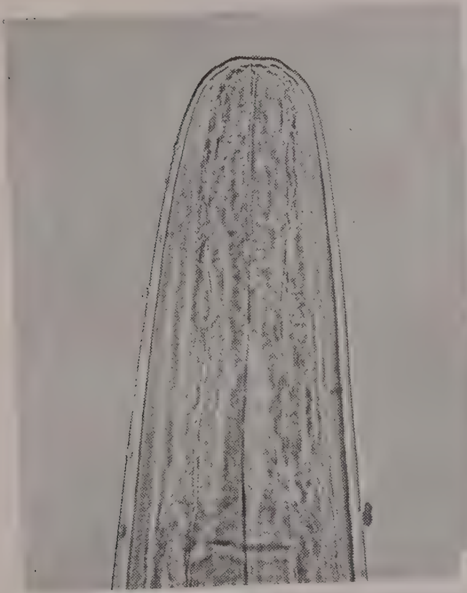

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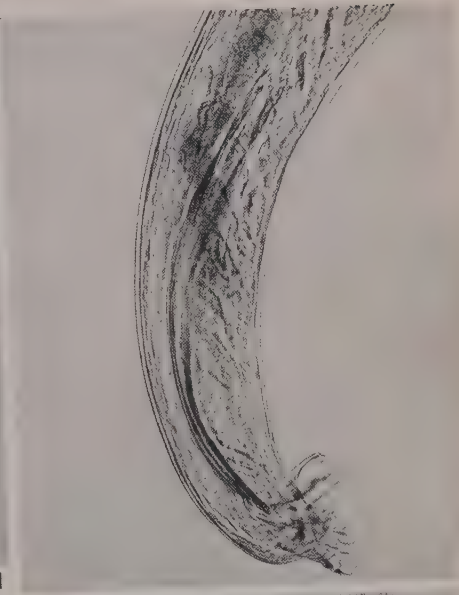

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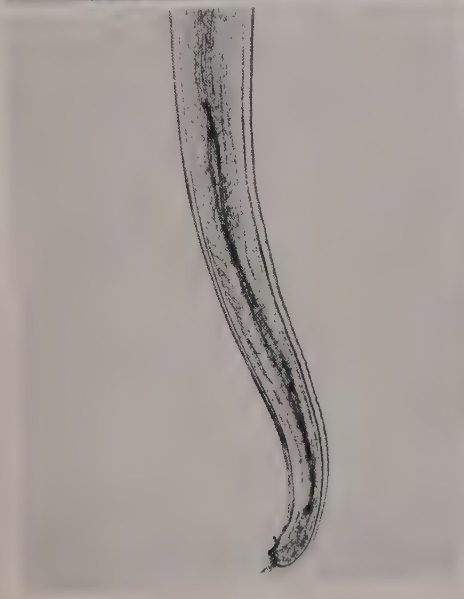

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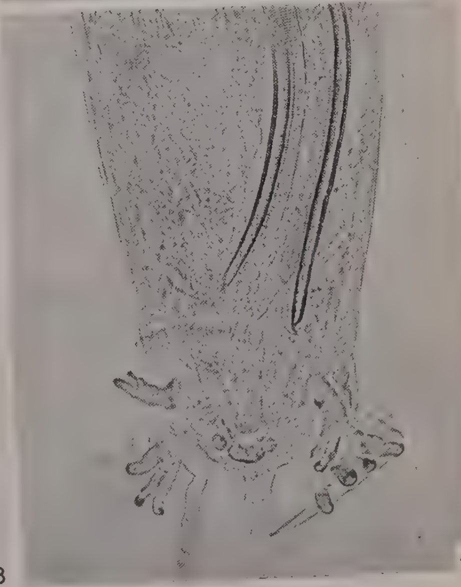

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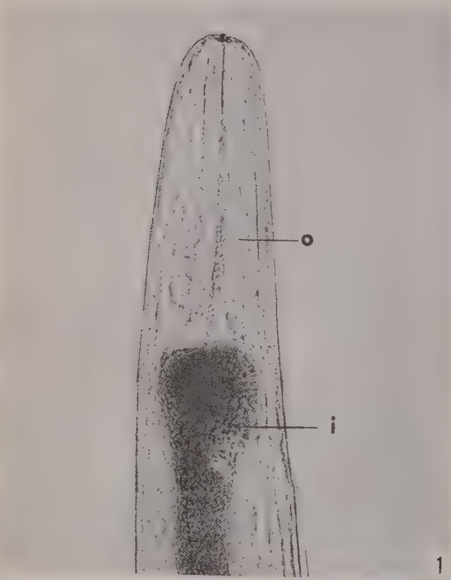

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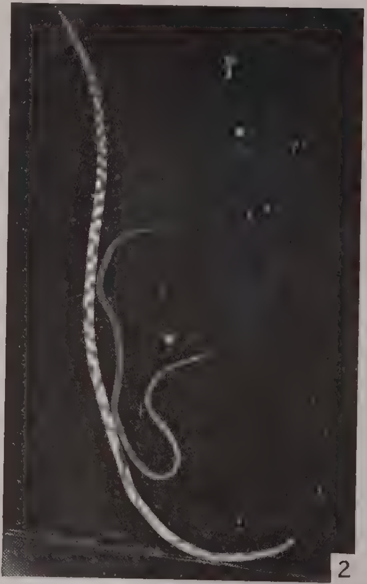

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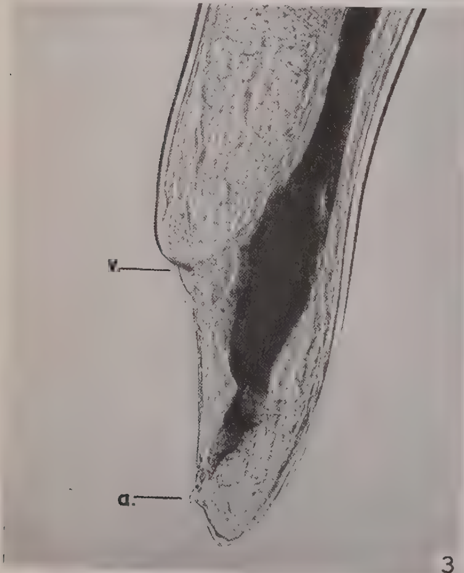

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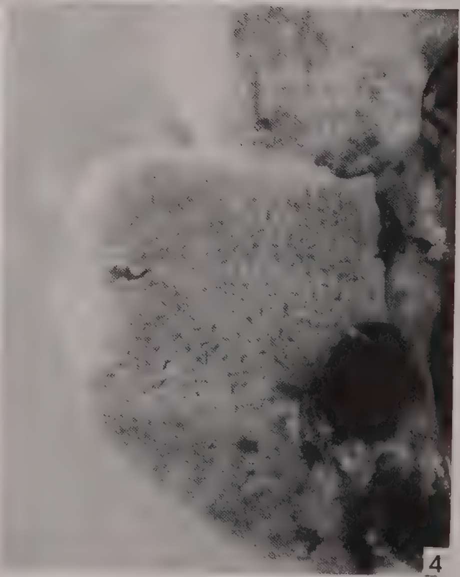

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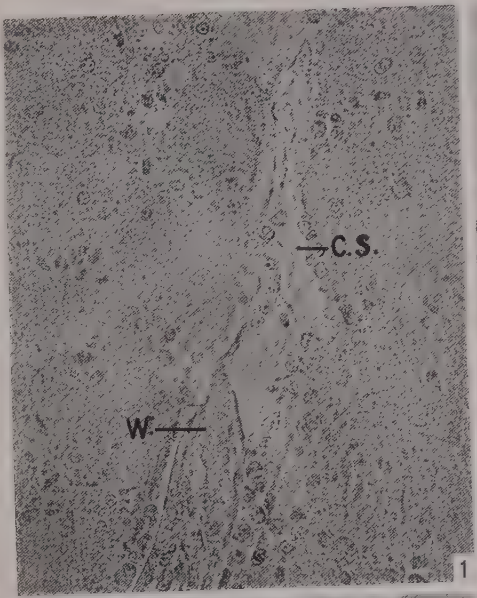

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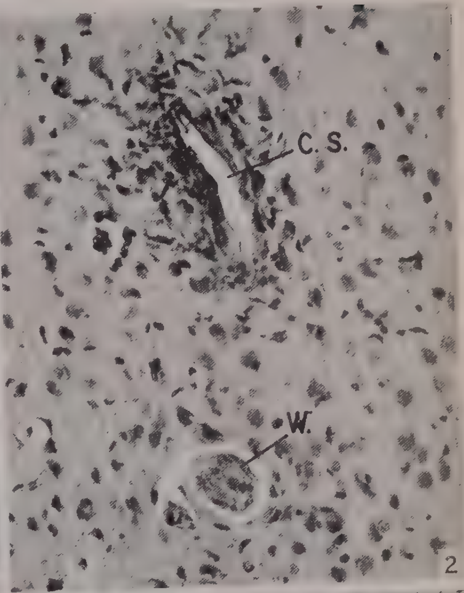

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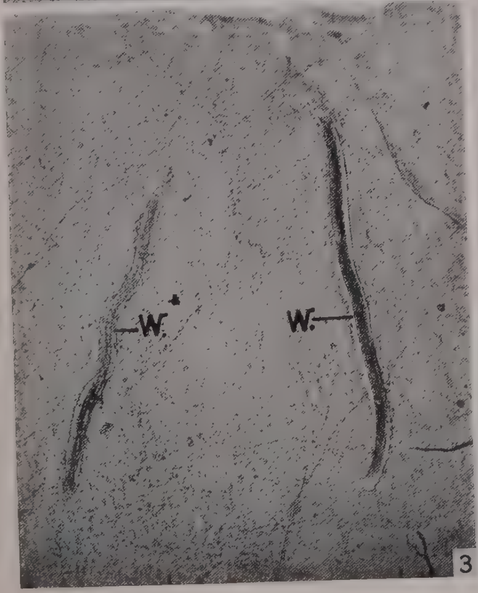

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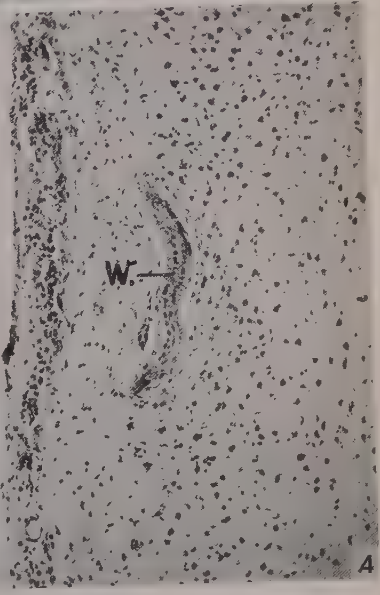

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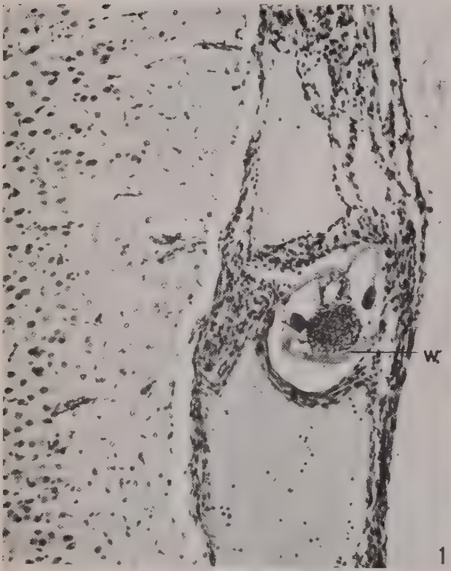

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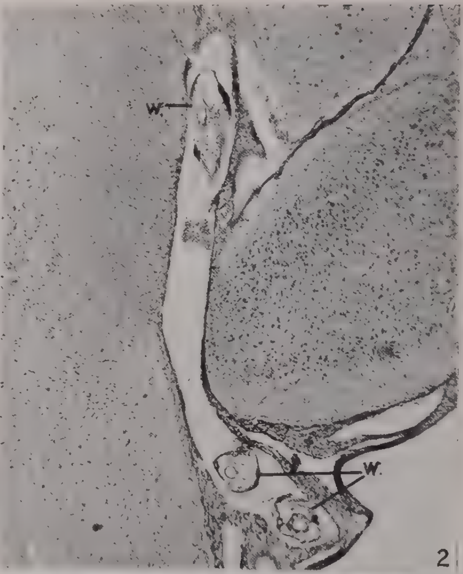

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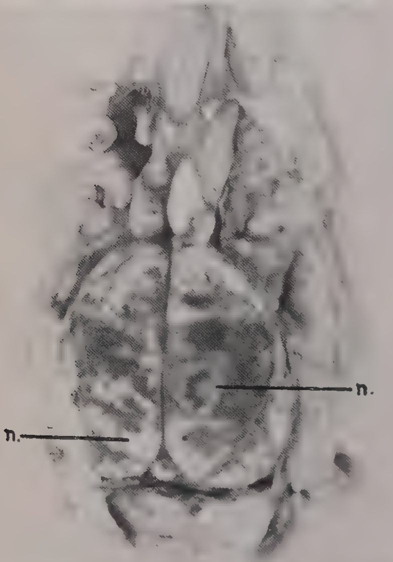

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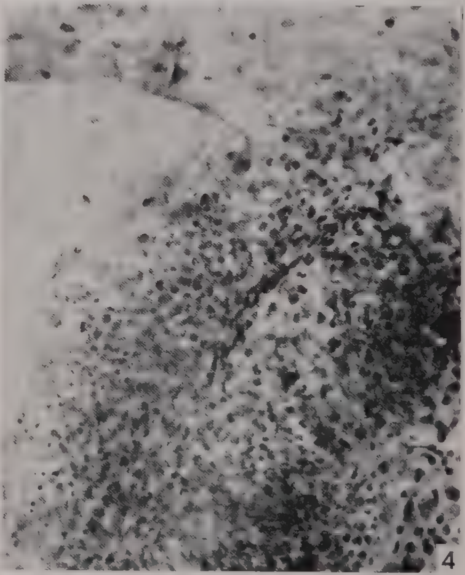

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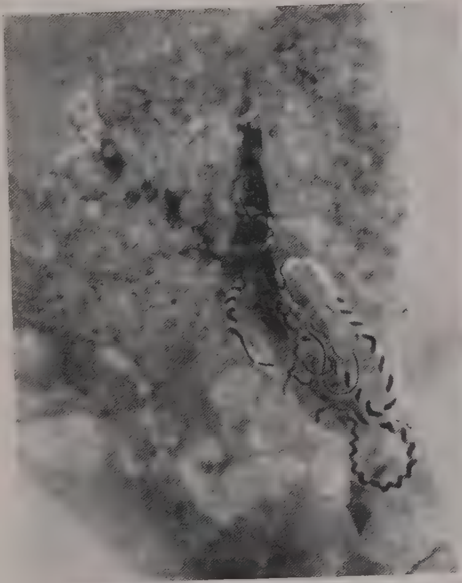

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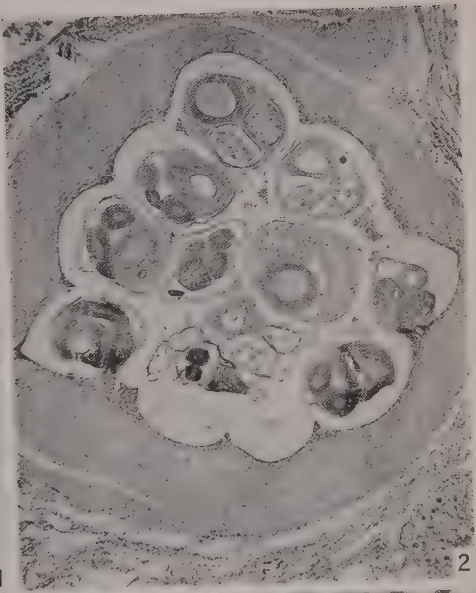

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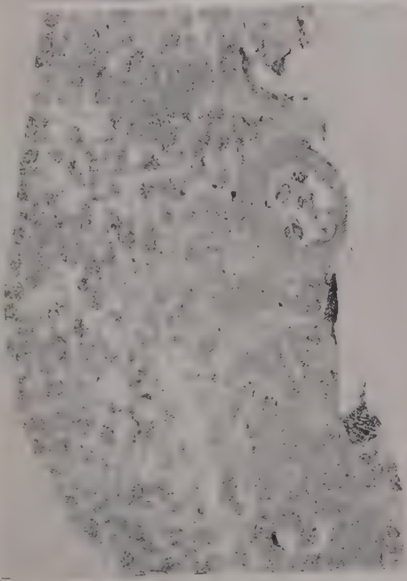

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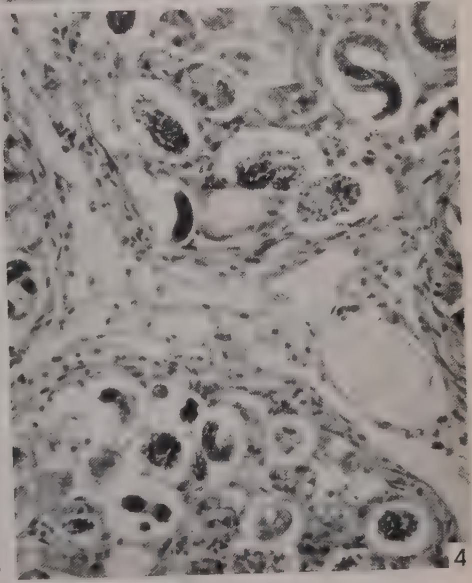

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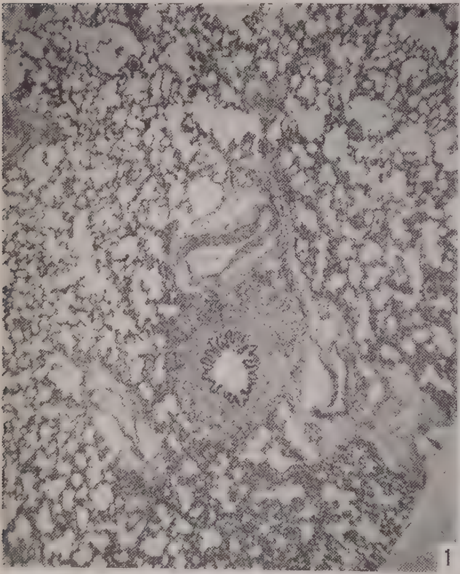

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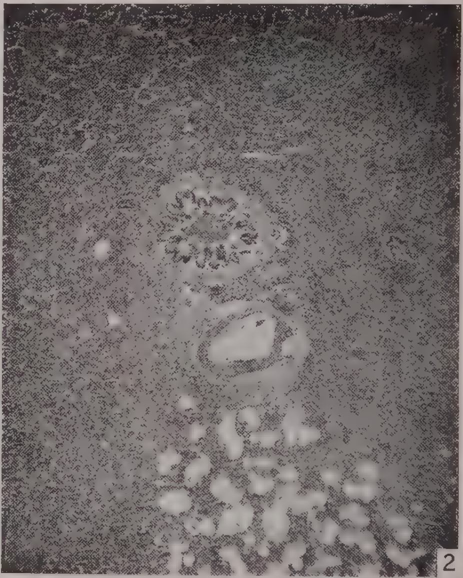

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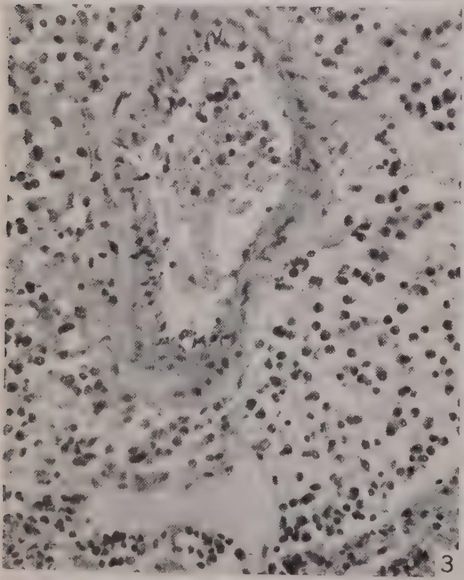

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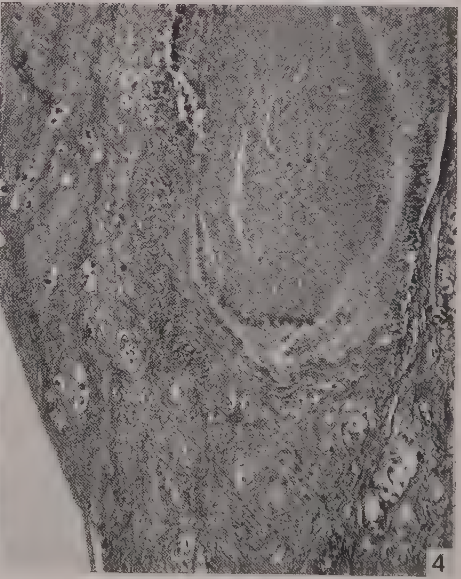

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EXPLANATION OF PLATES 1-6

PLATE 1

Fig. 1.—Anterior end of male. × 280.
Fig. 2.—Posterior end of male (Brisbane specimen). × 140.
Fig. 3.—Posterior end of male (Innisfail specimen). × 55.
Fig. 4.—Posterior end of male, ventral view. × 280.

PLATE 2

Fig. 1.—Anterior end of female. × 140.
Fig. 2.—Living male and female. × 3.
Fig. 3.—Posterior end of female. × 140.
Fig. 4.—Normal lung above, infected lung below, unfixed. × 3.3.
(Lettering as in Fig. 10.)

PLATE 3

Fig. 1.—Third moult, cerebrum, seventh day. × 280.
Fig. 2.—T.S. cerebrum, seventh day, absorption of cast skin. × 280.
Fig. 3.—Fourth-stage larvae, cerebrum, 11th day. × 40.
Fig. 4.—T.S. cerebrum, 12th day, portion of worm and early meningeal reaction. × 140.
(Figs. 1 and 3 are from fixed, but unstained, squash preparations. *c.s.*, Cast skin, *w.*, worm.)

PLATE 4

Fig. 1.—T.S. cerebrum, 29th day, showing worm (*w.*) in meninges. × 140.
Fig. 2.—T.S. cerebrum, 29th day, showing worm (*w.*) in vein. × 40.
Fig. 3.—Brain in situ, dorsal view, 31st day, necrotic areas (*n*). × 2.2.
Fig. 4.—Cerebrum of mouse, 26th day, phagocytosis of dead worm. × 280.

PLATE 5

Fig. 1.—Dissected lung, showing living worms. × 3.8.
Fig. 2.—T.S. lung, showing worms in artery. × 40.
Fig. 3.—T.S. lung, natural infection. × 10.
Fig. 4.—T.S. lung, showing segmenting ova. × 240.

PLATE 6

Fig. 1.—T.S. lung, 29th day, commencing oedema. × 40.
Fig. 2.—T.S. lung, 33rd day, extensive exudate. × 40.
Fig. 3.—T.S. same lung as in Figure 2, showing periarterial, leucocytic infiltration. × 280.
Fig. 4.—T.S. lung, 293rd day, fibrosis and necrosis. × 40.

THE EFFECT OF LIGHT AND TEMPERATURE ON THE RHYTHM OF PUPAL ECDYSIS IN THE QUEENSLAND FRUIT-FLY, *DACUS* (*STRUMETA*) *TRYONI* (FROGG.)

By M. A. Bateman*

(*Manuscript received July* 8, 1954)

Summary

Adults of the Queensland fruit-fly, *Dacus* (*Strumeta*) *tryoni*, show a pronounced diurnal rhythm in pupal ecdysis.

Experiments are described which show that the rhythm can be induced and oriented by alternation of light and darkness during the larval stage or the adult stage of the previous generation.

The alternation of light and darkness during the pupal stage had no direct effect on the rhythm of pupal ecdysis.

When pupae were exposed to a small daily fluctuation in temperature, the rhythm of ecdysis was more pronounced — i.e. ecdyses were spread over fewer hours of the day. Most of the flies emerged within a few hours after the initial increase in temperature.

I. Introduction

Diurnal rhythms of pupal ecdysis have been observed in many insects, but experimental investigations of the phenomenon have been done in comparatively few. These include *Ephestia kuhniella* (Bremer 1926; Scott 1936); *Rhabdophaga terminalis* (Barnes 1930); *Scatophaga stercoraria* (Lewis and Bletchly 1943); and *Drosophila* (Bunning 1935; Kalmus 1940). At least in *Scatophaga* and *Drosophila*, light has been found to influence the time of pupal ecdysis (see discussion).

Myers (1952) observed that adults of the fruit-fly, *Dacus tryoni*, kept in laboratory cultures at approximately 75°C, and 73 per cent. relative humidity, and under artificial illumination from 9 a.m. to 5 p.m. each day, tended to emerge from their puparia only during the mornings; 97 per cent. emerged between 8 a.m. and 2 p.m. Since temperature was kept fairly constant during these experiments, it seemed probable that the rhythm of ecdysis was associated with the daily alternation of light and darkness. Experiments have therefore been done to see if the rhythm could be modified by varying the time of day at which the pupae, the larvae, and the previous generation of adults were illuminated. One experiment was done which showed that the rhythm of ecdysis was modified when the pupae were exposed to small daily fluctuations in temperature.

Throughout this paper the term "diurnal rhythm" is used to denote a phenomenon which recurs once every 24 hr. The term "persistent rhythm" denotes a rhythm which is maintained even though such components of the environment as light, temperature, and humidity are kept

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constant. A "non-persistent rhythm" is one which is controlled directly by fluctuations in some component of the environment, and which disappears when these fluctuations cease.

II. Materials and Methods

Extensive stock cultures of *D. tryoni* were kept throughout the investigation in a constant-temperature room at 26.6 ± 2°C, and 75 ± 10% relative humidity. In the day-time (9 a.m. to 4.45 p.m.) they were kept in front of fluorescent tubes, giving an illuminance in the cages of 240 lumens/sq. ft. From 4.45 p.m. to 5.15 p.m. each day, the illuminance was reduced to approximately 1 lumen/sq. ft., since these flies do not copulate in bright light. At night (5.15 p.m. to 9 a.m.), the flies were kept in complete darkness.

Adult flies were fed on sugar, water, and a proprietary product called "M.R.T." which is a protein hydrolysate of yeast.*

When pupae were required for experiments the flies in the stock cultures were allowed to lay their eggs into ripe pawpaw fruit (*Carica papaya*). Preliminary experiments showed that when the larvae developed at fairly high density (about 200 larvae per pound of fruit), variability in the length of larval life was considerably reduced. This procedure therefore ensured that the pupae in any single experiment were of a uniform age, and that the period during which the adults emerged was reduced to a minimum.

During experiments, the pupae were kept in incubators at constant temperature (26.6 ± 0.1°C), and over 90 per cent. relative humidity.

In experiments in which pupae were kept in constant darkness, observations on the rhythm of ecdysis were made in the following way. Single pupae were placed on small metal disks, 1 cm in diameter, soldered to metal grids which replaced the shelves of a light-proofed incubator, which was housed in a darkroom. Beneath each grid was placed a tray made of galvanized iron which had been thinly coated on its upper surface with a "tanglefoot" preparation. As each fly struggled to emerge from its puparium it rolled off its disk and was caught in the tanglefoot immediately beneath. At the end of each hour during the period when the flies were emerging, the lights in the darkroom were switched off, the doors of the incubator were opened, and the tanglefoot trays were removed from the incubator and replaced by others which had been cleared of emerged flies.

In experiments in constant light, pupae were kept in an incubator with a glass door and artificial light was supplied by a 100-W incandescent lamp. They were protected from radiant heat by a piece of heat-absorbent glass ("Chance ON-19") suspended in front of the lamp. The pupae were set out in small glass petri dishes arranged so that the distance between each dish and the lamp was approximately 50 in. Observations were made each hour by simply counting the number of newly emerged flies in each petri dish.

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* Obtained from Marvin R. Thompson Pty. Ltd., Stamford, Connecticut, U.S.A.

In experiments in which pupae were kept for part of the day in light and the rest in darkness, use was made of two incubators, one being kept in complete darkness, the other in constant light. The pupae were kept in glass petri dishes and were transferred from one incubator to the other at the appropriate times. This arrangement was necessary to avoid the effects of heat radiation from the incandescent lamp, which would have caused a sudden increase in the temperature of the pupae when the light was switched on, and a corresponding fall when the light was switched off, if the pupae had been kept in a single incubator.

The thermostats of the incubators were adjusted so that a "black-bulb" thermometer (held where the pupae were to be placed) gave a reading of 26.6°C in each incubator despite the differences in illumination.

In these experiments observations in the light were made by simply counting the numbers of adults in each petri dish; observations in the dark were made with the aid of dull red light, after preliminary experiments had shown that this procedure did not effect the rhythm of ecdysis.

III. DESIGN OF EXPERIMENTS

The following is a plan of the experiments:

A. The effect of light on the ecdysis of pupae when larvae were kept in the dark.
   1. Pupae were kept in constant darkness.
   2. Pupae were kept in constant light.
   3. Pupae were kept in light from 9 a.m. to 5 p.m. and in darkness from 5 p.m. to 9 a.m.
   4. Pupae were kept in darkness from 9 a.m. to 5 p.m. and in light from 5 p.m. to 9 a.m.

B. The effect of light during the larval stage on the ecdysis of pupae.
   1. Larvae were kept in light from 9 a.m. to 5 p.m. and in darkness from 5 p.m. to 9 a.m. Pupae were kept in constant darkness.
   2. Larvae were kept in darkness from 5 a.m. to 9 p.m. and in light from 9 p.m. to 5 a.m. Pupae were kept in constant darkness.
   3. Larvae were kept in light from 9 a.m. to 5 p.m. and in darkness from 5 p.m. to 9 a.m. Pupae were kept in constant light.
   4. Larvae were kept in darkness from 5 a.m. to 9 p.m. and in light from 9 p.m. to 5 a.m. Pupae were kept in constant light.

C. The effect of light during the adult stage on the ecdysis of pupae in the subsequent generation.
   1. Adults were kept in light from 9 a.m. to 5 p.m. and in darkness from 5 p.m. to 9 a.m. Larvae and pupae were kept in constant darkness.

2. Adults were kept in darkness from 5 a.m. to 9 p.m. and in light from 9 p.m. to 5 a.m. Larvae and pupae were kept in constant darkness.
3. Adults were kept in light from 9 a.m. to 5 p.m. and in darkness from 5 p.m. to 9 a.m. Larvae were kept in constant darkness, and pupae in constant light.
4. Adults were kept in darkness from 5 a.m. to 9 p.m. and in light from 9 p.m. to 5 a.m. Larvae were kept in constant darkness and pupae in constant light.

D. The effect of small daily fluctuations in temperature during pupal development, on the rhythm of pupal ecdysis.

IV. Results

The results of all the experiments listed in the previous section are summarized in 14 histograms (Figs. 1-6). The number of ecdyses recorded for each experiment and the mean hours of ecdysis are presented in Table 1.

Table 1

MEAN HOURS AT WHICH ECDYSES OCCURRED, AND NUMBER OF ECDYSES RECORDED IN EACH EXPERIMENT

Experiments	Figure	Mean Hour of Ecdysis	Number of Ecdyses
Larvae and pupae in constant darkness	1*A*	12.30 p.m.	156
Pupae in constant light; larvae in constant darkness	1*B*	1.45 p.m.	262
Pupae in light from 9 a.m. to 5 p.m.; larvae in constant darkness	1*C*	1.45 p.m.	536
Pupae in light from 5 p.m. to 9 a.m.; larvae in constant darkness	1*D*	12.30 p.m.	488
Larvae in light from 9 a.m. to 5 p.m.; pupae in constant darkness	2*A*	1.00 p.m.	89
Larvae in light from 9 p.m. to 5 a.m., pupae in constant darkness	2*B*	8.00 p.m.	104
Larvae in light from 9 a.m. to 5 p.m.; pupae in constant light	3*A*	9.25 a.m.	199
Larvae in light from 9 p.m. to 5 a.m.; pupae in constant light	3*B*	7.50 p.m.	203
Previous adults in light from 9 a.m. to 5 p.m.; larvae and pupae in constant darkness	4*A*	12.30 p.m.	156
Previous adults in light from 9 p.m. to 5 a.m.; larvae and pupae in constant darkness	4*B*	12.50 a.m.	214
Previous adults in light from 9 a.m. to 5 p.m.; larvae in constant darkness, pupae in constant light	5*A*	1.45 p.m.	262
Previous adults in light from 9 p.m. to 5 a.m.; larvae in constant darkness, pupae in constant light	5*B*	1.30 a.m.	289

The results of the four experiments carried out to determine the effect of light during the pupal stage on the rhythm of ecdysis are compared in Figure 1. These histograms show quite clearly that the time at which ecdysis occurred was entirely independent of the conditions of illumination during pupal development. In each experiment over 80 per cent. of the flies emerged between 6 a.m. and 6 p.m., regardless of whether the pupae were kept in constant darkness, constant light, or alternating light and darkness.

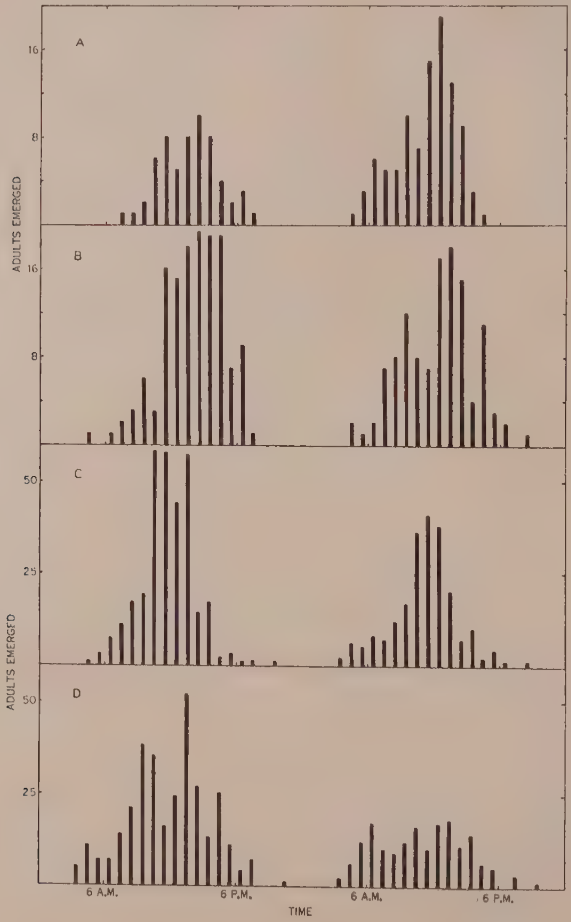

Fig. 1.—Rhythms of ecdysis when larvae developed in constant darkness and pupae were kept in: *A*, constant darkness; *B*, constant illumination; *C*, light during the day and darkness at night; *D*, darkness during the day and light at night.

Graphs *A* and *B* in Figure 1 show also that the rhythm of ecdysis in *D. tryoni* is a "persistent rhythm" since it was maintained even though light, temperature, and humidity were kept constant.

Figure 2 shows the way in which the time of ecdysis of pupae kept in constant darkness was modified by altering the time at which the developing larvae were illuminated. In Figure 2*A* the larvae were kept in the light from 9 a.m. to 5 p.m. and in darkness the rest of the day, and the adults emerged only between 6 a.m. and 5 p.m.: in Figure 2*B* the larvae were kept in darkness during the day (9 a.m. to 5 p.m.) and light at night, and the adults emerged only between 2 p.m. and 2 a.m.

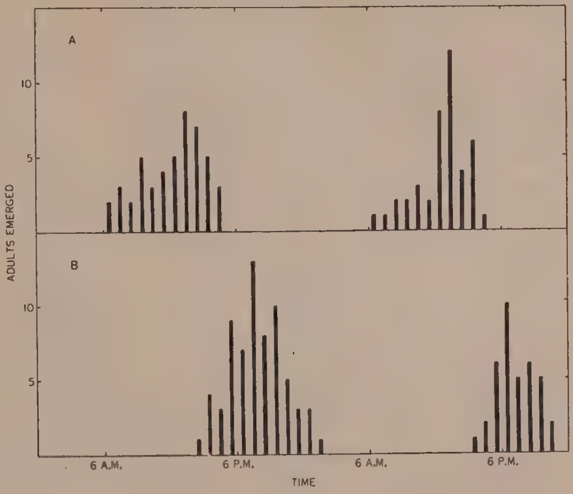

Fig. 2.—Effect of illumination during the larval stage on the ecdysis of pupae kept in constant darkness: *A*, larvae illuminated from 9 a.m. to 5 p.m.; *B*, larvae illuminated from 9 p.m. to 5 a.m.

Figure 3 shows the results of two further experiments on the effect of light on the larvae. These experiments were the same as those illustrated in Figure 2, except that the pupae were kept in constant illumination. When larvae were illuminated from 9 a.m. to 5 p.m., 88 per cent. of adults emerged from their puparia between 6 a.m. and 6 p.m. (Fig. 3*A*). When larvae were illuminated from 9 p.m. to 5 a.m., all adults emerged between 12 noon and 12 midnight (Fig. 3*B*).

The results of these four experiments (Figs. 2, 3) show that there was a definite correlation between the time of day when the developing larvae were illuminated and the time at which ecdysis occurred in the pupae. When larvae were exposed to light in the day-time and kept in darkness at night, the adults tended to emerge during the day. When larvae were exposed to light during the night and kept in darkness during the day, the adults tended to emerge during the night.

During these experiments alternating light and darkness for the larvae was obtained by keeping the pawpaws in which they were developing in a constant-temperature room in front of fluorescent lights which were switched on or off at the appropriate times. Radiant heat from the lights caused a gradual increase in the temperature of the pawpaws, of 2.4°C (from 25.6 to 28.0°C) during a period of 8 hr illumination. It is possible therefore that the rhythm impressed on the developing larvae was not due to the fluctuations in illuminance, but to the accompanying regular fluctuations in temperature. This possibility, however, can be discounted by evidence obtained from experiments whose results are set out in Figure 1. In all these experiments the developing larvae were kept in constant darkness, the infested pawpaws being kept in a screened-off section of the constant-temperature room. Subsequent observation showed that, owing to inadequate control of temperature in the room, these larvae were exposed to temperatures which were 3°C higher during the night than during the day. If temperature changes during the larval stage could influence the rhythm of pupal ecdysis, it would be expected that the period of maximum ecdysis would be correlated with the time at which the larvae were subject to maximum temperatures. In none of these experiments was this so: maximum temperatures during the larval stage occurred at night, while maximum pupal ecdysis occurred during the day-time.

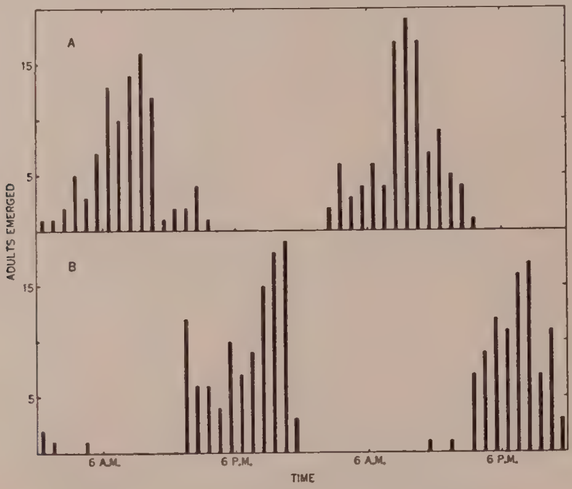

Fig. 3.—Effect of illumination during the larval stage on the ecdysis of pupae kept in constant light: *A*, larvae illuminated from 9 a.m. to 5 p.m.; *B*, larvae illuminated from 9 p.m. to 5 a.m.

Thus it is probably safe to ignore these changes in temperature and to conclude that the regular alternation of light and darkness during the larval stage induced the rhythm of pupal ecdysis. The period of these fluctuations in illuminance was apparently impressed on the developing larvae in such a way that it persisted throughout pupal development and determined the time at which the adults emerged from their puparia.

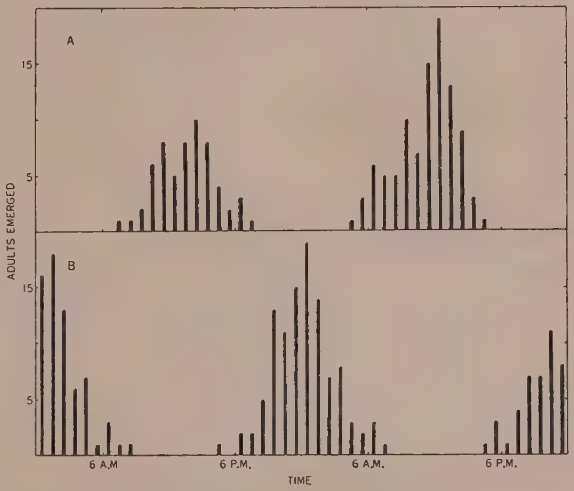

Fig. 4.—Effect of light during the imaginal stage on the pupal ecdysis of the subsequent generation (larvae and pupae kept in constant darkness): *A*, adults illuminated from 9 a.m. to 5 p.m.; *B*, adults illuminated from 9 p.m. to 5 a.m.

Figures 4 and 5 show the results of four experiments which were carried out to determine if a rhythm of pupal ecdysis could be induced by an effect of light on the adults of the previous generation. The graphs show quite clearly that the rhythm of ecdysis was reversed by reversing the times at which adults of the previous generation were exposed to light and darkness. When adults were kept in the light from 9 a.m. to 5 p.m. each day, and in darkness during the night, 95 per cent. of their progeny emerged between 6 a.m. and 6 p.m. When adults were kept in light from 9 p.m. to 5 a.m. each night, and in darkness during the day, 90 per cent. of their progeny emerged between 6 p.m. and 6 a.m. In all of these experiments the developing larvae were kept in complete darkness.

The importance of temperature changes in the determination of the time of pupal ecdysis in *D. tryoni* is illustrated in Figure 6. In this experiment pupae were kept throughout their development in the constant-temperature room in front of fluorescent lights which were switched on at

9 a.m. and off at 5 p.m. each day. Changes in temperature were measured by means of a "black-bulb" thermometer, read at half-hourly intervals.

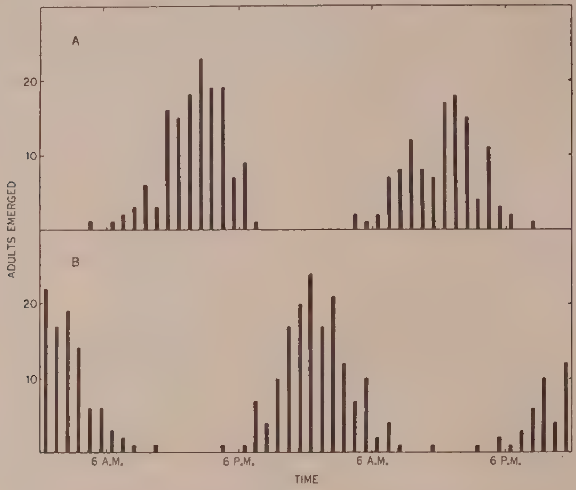

Fig. 5.—Effect of light during the imaginal stage on the pupal ecdysis of the subsequent generation (larvae kept in constant darkness and pupae kept in constant light): *A*, adults illuminated from 9 a.m. to 5 p.m.; *B*, adults illuminated from 9 p.m. to 5 a.m.

Under these conditions ecdyses were restricted to a period of 7 hr each day (from 7 a.m. to 2 p.m.). When changes in temperature due to radiation of heat from the light-source were prevented, ecdyses were spread over 19 hr, from 3 a.m. to 10 p.m. (see Fig. 1*C*).

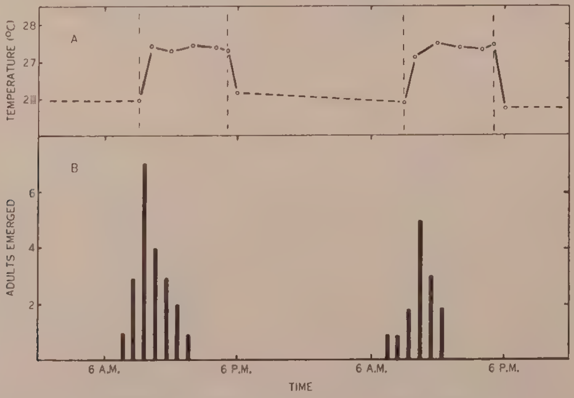

Fig. 6.—Effect of small changes in temperature on the rhythm of pupal ecdysis: *A*, changes in temperature; *B*, rhythm of pupae illuminated from 9 a.m. to 5 p.m. (previous larvae were kept in constant darkness).

V. DISCUSSION

The importance of light in the initiation and orientation of rhythms of pupal ecdysis has been demonstrated for several insects besides *D. tryoni*. Persistent and inherited rhythms of ecdysis, induced by the daily alternation of light and darkness have been shown in *Drosophila* (Bünning 1935; Kalmus 1940), and in the dung-fly, *Scatophaga stercoraria* (Lewis and Bletchly 1943).

Bünning demonstrated persistence in the rhythm of ecdysis in *Drosophila*. He reared flies in constant dim illumination and found that the rhythm lasted for several generations. Kalmus found that a single period of illumination, provided it lasted at least 4 hr, induced a 24-hr rhythm of pupal ecdysis in a culture of *Drosophila* kept before and after in complete darkness.

Lewis and Bletchly (1943) found that the rhythm of ecdysis in *Scatophaga stercoraria* persisted when pupae were kept in constant light or constant darkness, but was more pronounced (i.e. ecdyses were spread over fewer hours of the day) when the pupae were exposed to "natural" daylight and darkness. They concluded therefore that the rhythm is persistent and inherited, but that the natural daily alternation of light and darkness contributes to the control of the rhythm by a direct effect on the pupae.

Two instances where non-persistent rhythms of ecdysis were oriented directly by light have been reported in the literature. Barnes (1930) found that when pupae of the gall midge *Rhabdophaga terminalis* were exposed to natural lighting, 92 per cent. of ecydses occurred before 12 noon. But when pupae were kept in darkness until 12 noon and then illuminated until 8 p.m. each day, only 72 per cent. of ecdyses occurred before 12 noon. Phillipp (1938) found that the rhythm of ecdysis in *Chironomus* was determined directly by the daily alternation of light and darkness, and did not persist in constant conditions.

The experiments in this paper showed that the rhythm of ecdysis in *D. tryoni* is similar to those reported for *Drosophila* and *Scatophaga* in that it persisted even when the pupae were kept in constant temperature and humidity and constant light or darkness. It differed from *Scatophaga* in that light had no direct effect on the pupae in *D. tryoni;* the rhythm could not be altered by altering the time of day at which the pupae were exposed to light (see Fig. 1).

Little seems to be known about the physiology of the persistence of rhythms of this type. The most widely accepted view appears to be that the apparent time sense involved is due to periodic fluctuations in metabolic rate (Bünning 1935). Kalmus (1940) examined the effect of different constant temperatures on the intervals between peaks of pupal ecdysis in *Drosophila* and found that the intervals could be lengthened to as much as 2½ days by low temperatures, and shortened to 16 hr by high temperatures. These results indicate that the internal "clock" which orients the rhythm of ecdysis in the absence of external periodic stimulation is chemical in nature, and is probably related to metabolic rate. Kalmus showed also that the diurnal rhythm of activity of axolotl larvae disappeared in constant darkness when the pituitary was removed. He suggested that periodic secretion of a hormone was responsible for the persistence of this rhythm.

The results presented in Figures 4 and 5 show that in *D. tryoni* the time of pupal ecdysis can be determined as far back in the life cycle as the adults of the previous generation. The rhythm impressed on the adults by the alternation of light and darkness was "inherited" by their progeny and was retained throughout embryonic, larval, and pupal development. The mechanisms by which characters of this sort are passed from parent to offspring are not well understood. The cytoplasm alone may be involved, and in this case also, periodicity may be maintained in the egg by means of fluctuations in metabolic rate. However, there is as yet no experimental evidence to substantiate this hypothesis.

The results presented in Figure 6 show that a relatively small increase in temperature had a marked effect on the rhythm of ecdysis in *D. tryoni.* In view of this it seems likely that where the fly is breeding in orchards, or exposed situations, the inherent rhythm of ecdysis may be greatly affected by the daily cycle of temperature.

It is interesting to note, however, that the native fruits, in which *D. tryoni* bred before cultivated fruits were introduced into Australia, occurred mainly in thick rain-forests which covered large areas of Queensland and northern New South Wales. In these rain-forests the soil is usually quite moist and completely shaded from the sun by the dense canopy overhead, and its temperature 2-3 in. below the surface (where the pupae are found) must remain remarkably constant throughout each 24 hr. In such situations a persistent rhythm of ecdysis, induced and oriented by the daily alternation of light and darkness during previous stages in the life history of the fly, may have survival value, since it would ensure that the newly formed adults emerged from their puparia during the hours of daylight.

VI. ACKNOWLEDGMENTS

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STUDIES ON MARSUPIAL REPRODUCTION

I. GENERAL FEATURES AND TECHNIQUES

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(*Manuscript received June* 16, 1954)

Summary

Previous work on the reproduction of marsupials is mentioned briefly and the taxonomy of *Setonix brachyurus* Quoy and Gaimard, the animal chosen for this investigation, is discussed. The feeding in captivity, surgery, methods of taking vaginal smears, and histological methods are described.

Anatomically the reproductive system of *Setonix* is similar to that of other marsupials. There are two ovaries, two uteri, and two lateral vaginae. The vaginal culs-de-sac are connected to the urogenital sinus, forming a pseudo-vaginal canal which remains open after the birth of the first young. The reproductive system differs from that of the true kangaroos and resembles that of the rat kangaroos in possessing an anterior vaginal expansion.

Some preliminary observations on breeding are recorded, with some details of growth rates, feeding, etc. of pouch young.

I. Introduction

The reproductive physiology of only one marsupial species (*Didelphis virginiana*) is really well known. Although Hill and O'Donoghue's (1913) paper predated the publication of Hartman's (1923) work on the American polyprotodont opossum (*Didelphis*) the ensuing period has seen little advance in systematized knowledge of reproduction in Australian species. Hill and O'Donoghue (1913) found the polyprotodont marsupial *Dasyurus* to be monoestrous in contrast to the polyoestrous condition subsequently found by Hartman in *Didelphis*. Flynn (1930) was able to demonstrate a polyoestrous condition in the diprotodont *Bettongia*, but his paper deals mainly with uterine changes and has no data from animals breeding in captivity.

The present study was undertaken to provide information about a diprotodont to permit detailed comparison with information available about the polyprotodont *Didelphis*. The Rottnest Island wallaby, or 'quokka' (*Setonix brachyurus* Quoy and Gaimard), was selected because, although a slow breeder, it is accessible in quantity, easily domesticated, and of convenient size (*c.* 3 kg).

There is some uncertainty about the taxonomic position of *Setonix*. Most authors agree in separating this monospecific genus from the remaining genera of the macropods but its relationships are otherwise obscure. Bensley (1903) and Wood Jones (1924) both recognized the resemblance between the molar teeth of the quokka and those of the tree kangaroos

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(*Dendrolagus*). Whereas Bensley considered *Setonix* to have paralleled *Dendrolagus* in this respect, Wood Jones placed the two genera together in his classification. Troughton (1941), though recognizing its dental peculiarities, placed *Setonix* with the genus *Thylogale*. Tate (1948) considered *Setonix* a derivative of *Protemnodon* (*Wallabia*) and, according to his phylogenetic arrangement, more closely allied to *Wallabia* than to *Thylogale*. Cytologically the affinities of *Setonix* are with *Thylogale* rather than with *Wallabia*. Drummond (1933), confirmed by us, has shown the quokka to possess 22 chromosomes and *Thylogale billardierii* (considered by Troughton to be its nearest relative) has also 22 chromosomes (McIntosh and Sharman 1953). Five members of the genus *Wallabia* so far studied cytologically have chromosome numbers of 16 or (in one species) less. Nothing is known of the cytology of the tree kangaroos, but on the whole the evidence seems to favour placing *Setonix* close to scrub wallabies of the genus *Thylogale*.

II. ANIMAL HUSBANDRY AND LABORATORY TECHNIQUES

The department has compounds with suitable shelters, water troughs, and feed hoppers. Almost any feed mixture is suitable for the animals, the diet in captivity including green herbage, chaff, hay, and a concentrated stock ration (sheep nuts). The quokkas are captured in their island habitat during the night by manual netting. After transfer to the department compounds they rapidly gain in condition, no doubt because of improved feeding and abundant water.

Full aseptic conditions are necessary for surgery. Anaesthetization by intravenous injection is impossible as no surface veins can be located. It is best carried out by intraperitoneal injection of 'Nembutal' alone (80-100 mg/kg), or 'Dial' (50 mg/kg) followed by ether. Spaying cannot be performed by mid-ventral incision because of the disposition of pouch and pubic bones; it cannot be performed by dorsal approach because of the extensive sacrum. It can be done by either (*a*) making a crescentic skin incision between the vulva and the pouch, followed by fairly extensive dissection beneath the pouch to expose the body wall which can then be entered, or (*b*) via a lateral body approach. The former gives a better view of the uterus, but the latter is generally to be preferred because the wound is less difficult to keep clean subsequently.

A long urogenital sinus (Figs. 1, 2) separates the vaginae from the external genital opening so it is difficult to take vaginal smears. A vaginal smear substantially uncontaminated by the urogenital sinus lining can be taken from the region of the posterior vaginal sinus (*p.v.s.*, Fig. 2) by the following method. A tapered tube, open at both ends and about $\frac{1}{2}$ in. diameter at its thicker end, is inserted in the urogenital sinus. An ophthalmoscope light is held into the tube thus revealing the upper end of the sinus. The smear may then be taken by either of two methods: (*a*) insertion of a long metal catheter attached to a syringe of saline and extraction of cellular matter by suction; this may then be expressed on to a clean slide and immediately fixed for staining, or (*b*) a long hollow needle containing a wire looped at the end is inserted as far as possible, the wire is extruded from its inner end by pressure from the exterior. After a slight revolving motion the wire is withdrawn into the needle and the needle with its contained wire is removed. This second method is more tedious but prevents contamination of the smear, the wire loop being protected during both insertion and withdrawal by the enclosing needle. Vaginal smears are fixed in equal parts of ether and 95 per cent. alcohol and stained by the rapid method of Shorr (1941). This method gives satisfactory staining and differentiation once the worker is familiar with the technique.

For histological study of the various reproductive organs Bouin fixed material was sectioned and stained in haematoxylin with or without eosin counterstaining. Sections were usually cut at 7-12 μ but large organs were serially sectioned at 25 μ.

III. The Female Reproductive System

Figures 2 and 3 show the general anatomy of the female reproductive system.

(*a*) *Ovaries*

These are roughly 7 mm in diameter and are situated immediately anterior to, and in close contact with, the uteri (Fig. 1). This close connection is more apparent than real because the oviduct, though fairly long, is highly convoluted, and ovary, oviduct, and uterus lie in the same band of mesentery. Our records show that only one egg matures at a time and this is consistent with the observation that never more than one young is present in the pouch even immediately after parturition. Zuckerman (1953) has, however, recorded several sets of twins and one of triplets in macropod marsupials breeding in captivity.

During the growth of the Graafian follicles the cumulus oophoricus containing the developing oocyte remains for a time in contact with the developing membrana granulosa by slender trabeculae. This is also the case in *Didelphis* and in the rabbit (Martinez-Esteve 1942). In most other respects there is a general similarity between follicles of the quokka and those of the American opossum. The number of cell layers in cumulus and membrana granulosa and the exceedingly thin zona pellucida appear similar in both animals. The mature Graafian follicle in *Setonix* (Plate 1, Fig. 1) has a diameter of approx. 2.8 mm whilst mature follicles of the opossum (judged from Martinez-Esteve's photographs) are somewhat smaller. The diameter of the mature ovarian egg in *Didelphis* is 150 μ (Hartman 1916) whereas tubal ova average about 110 μ after fixation and staining. The diameter of the ovarian oocyte in *Setonix* at the time of the extrusion of the first polar body is 120-130 μ and the diameter of the fixed tubal egg, after fertilization but before fusion of pronuclei, is 140 μ. In contrast to these sizes given for marsupial eggs, the eggs of the mouse and Rhesus monkey are both less than 100 μ diameter when measured without the corona radiata. In the monotremes — platypus and echidna — the ovarian oocytes attain a diameter of almost 4 mm (Flynn and Hill 1939).

Ovulation is followed by collapse of the follicle and the growth of a corpus luteum. During development the corpus luteum usually has a space at the centre containing only connective tissue (Plate 1, Fig. 2). This space becomes entirely, or almost entirely, filled with luteal cells at full development when the diameter of the corpus luteum may exceed 4 mm.

The oviducts are lined by a single layer of columnar epithelium in which we have not been able to discern any ciliated cells.

(*b*) *Uteri*

These are fully separated fusiform bodies approx. 15 mm long. The usual layers — mesometrium, myometrium, and endometrium — are present (Plate 1, Fig. 7). The endometrium is 1-2 mm thick and except during anoestrus many well-developed uterine glands can be seen in a transverse section. The lumen and glands are lined by columnar epithelium which is one cell layer thick although the nuclei may be arranged in more than one layer.

(*c*) *Vaginal Complex*

From the common chamber into which the uterine necks open the several parts of the vaginal complex are given off. These are the anterior vaginal canals and the vaginal culs-de-sac. The anterior vaginal expansion is worthy of treatment in some detail since this structure is apparently unique in this group of marsupials. It is a short caecum lying between the uterine necks (Fig. 1) and is lined mainly by the stratified squamous epithelium typical of the vaginal complex (Plate 1, Fig. 7). Near the base of the expansion there is some infiltration of the columnar epithelium of the uterine necks. We are not sure whether the anterior vaginal expansion is homologous with the structure described by Pearson (1945, 1946, 1950) in the rat kangaroos. On the basis of the occurrence of an anterior vaginal expansion, and other specialized structures of the urogenital system, Pearson has elevated the rat kangaroos (Potoroidae) to family status distinct from the true kangaroos (Macropodidae, which includes *Setonix*). The occurrence of an anterior vaginal expansion in *Setonix* is then of considerable interest in view of the difficult taxonomic position of this genus.

The anterior vaginal canals arise from the common chamber and sweep forward and outward to pass at their most anterior point into the lateral vaginal canals. The lateral vaginal canals have a greater diameter and show a more strongly developed outer layer of circular muscle than the anterior vaginal canals. The lateral vaginal canals unite in a short posterior vaginal sinus (Fig. 2, *EF*) which opens into the urogenital sinus. Both anterior and lateral vaginal canals are lined with stratified squamous epithelium (Plate 1, Fig. 3) which may be cornified or non-cornified according to the stage of the oestrous cycle.

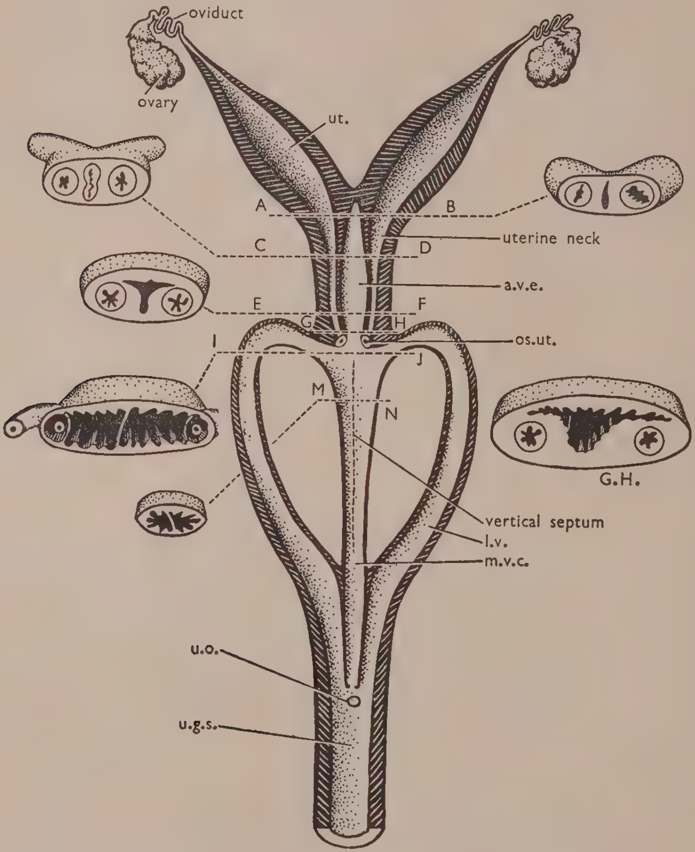


Fig. 1.—The urogenital system of *Setonix brachyurus*. The various transverse sections *AB*, *CD*, etc. are not drawn to scale. *a.v.c.*, anterior vaginal canal; *a.v.e.*, anterior vaginal expansion; *bl.*, bladder; *cl.*, clitoris; *l.v.*, lateral vagina; *m.v.c.*, median vaginal cul-de-sac; *os. ut.*, os uteri; *p.v.s.*, posterior vaginal sinus; *r.s.*, receptaculum seminis; *u.b.*, position of opening of ureter into bladder; *u.g.s.*, urogenital sinus; *u.o.*, position of opening of urethra into urogenital sinus; *ur.*, urethra; *ut.*, uterus.

The fused vaginal culs-de-sac in the non-parous animal reach almost to the urogenital sinus but an open pseudo-vaginal canal is not found prior to birth of the first young (cf. Plate 1, Figs. 6 and 8). The septum of the median vagina is complete from dorsal to ventral walls in the non-parous animal (Plate 1, Fig. 5) but does not extend to the anterior extremity of the common vaginal chamber so that the right and left culs-de-sac are connected at this point; neither does the septum reach the posterior end of the culs-de-sac and a common chamber is also found in this position (Plate 1, Fig. 6). Although the culs-de-sac are lined with the stratified squamous epithelium typical of the vaginal complex (Plate 1, Fig. 9) the posterior chamber is lined with a single layer of columnar cells (Plate 1, Fig. 10). This epithelium is similar to that at the opening of the uterine necks into the anterior common chamber so that it is probably of the same embryonic origin and has been carried to its posterior position by the growth of the culs-de-sac. At the first parturition the median septum is ruptured so that it is incomplete dorsoventrally in parous animals (Plate 1, Fig. 4). At the same time the tissue separating the posterior end of the culs-de-sac from the urogenital sinus is ruptured and the pseudo-vaginal canal thus formed remains open for the remainder of the life of the animal (Plate 1, Fig. 6).

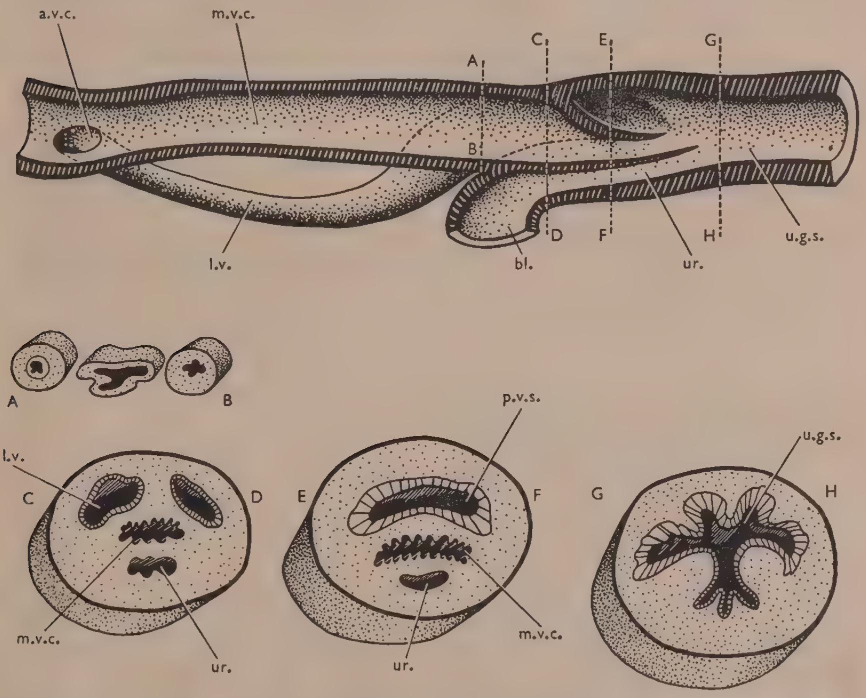


Fig. 2.—Longitudinal section of vaginal complex with cross sections at various levels. Symbols as in Figure 1.

Pearson (1950) has directed attention to the enormously distended anterior vaginal canals in certain macropods at oestrus. These serve as ducts for the reception of spermatozoa (Hill and Fraser 1925). Our own observations on *Macropus* (Sharman, unpublished data) are consistent with Pearson's demonstration that sperm are stored here, but how long they are stored is open to question. It is important to emphasize lack of information about this because it has sometimes been implied that prolonged storage of sperm in the female tract is the basis of delayed pregnancy in marsupials (Wood Jones 1944; Pearson and de Bavay 1953). In another paper (Sharman 1955) we have shown in fact that delayed pregnancy is achieved in another way.

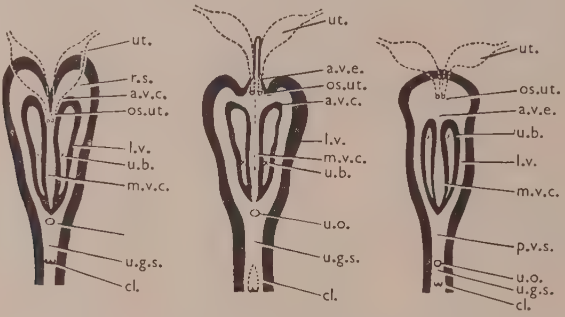
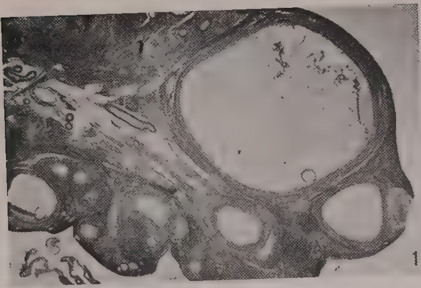


Fig. 3.—Comparison between the urogenital systems of (left) typical kangaroo, *Setonix brachyurus* (centre), and (right) rat kangaroo. Left and right hand figures redrawn after Pearson (1950). Symbols as in Figure 1.

In *Setonix* there is little or no hypertrophy of the anterior vaginal canals but there is a variable hypertrophy of the anterior vaginal culs-de-sac (cf. Plate 1, Figs. 4 and 5). We have noted sperm in the swollen anterior vaginal culs-de-sac of *Setonix* immediately after copulation but none have been found in the anterior vaginal expansion. So the condition in *Setonix* is not like that in the Potoroidae — in which the anterior vaginal expansion (Fig. 3*C*, *a.v.e.*) acts as a receptaculum seminis (Pearson 1950) — or to the condition in most macropods where the anterior vaginal canals serve the same function.

Apart from the presence of the anterior vaginal expansion the anatomy of the reproductive system in *Setonix* resembles that of other kangaroos (Macropodidae). As in the kangaroos the reproductive system differs from that of the rat kangaroos (Potoroidae) in the possession of a short posterior vaginal sinus and urethra, and a long urogenital sinus. The anatomy of the reproductive systems of kangaroos and rat kangaroos are compared with that of *Setonix* in Figure 3.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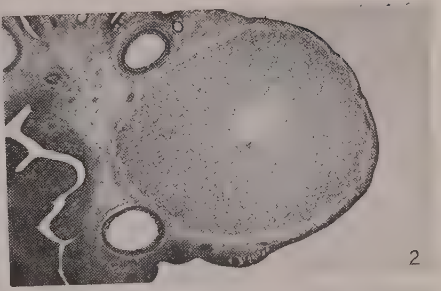
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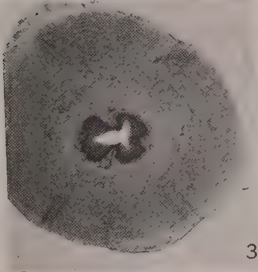
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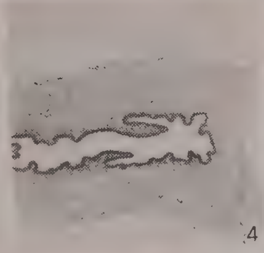
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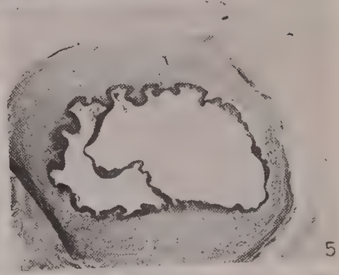
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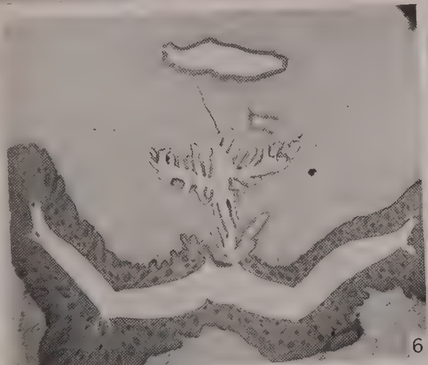
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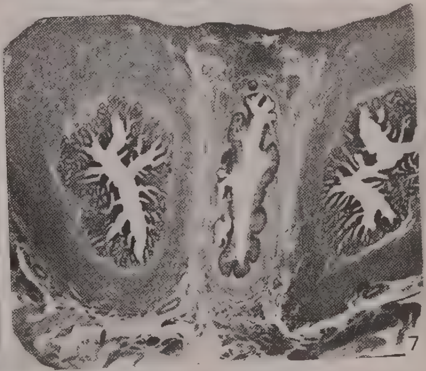
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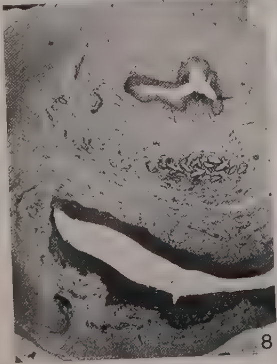
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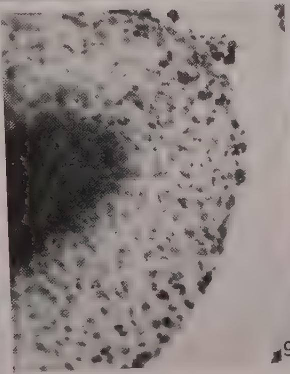
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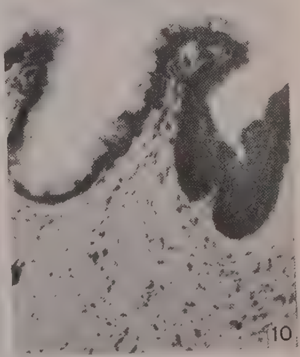
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(*d*) *Urogenital Sinus*

The urethra and posterior vaginal sinus open into the urogenital sinus as shown in Figures 1 and 2. All are lined with stratified squamous epithelium at all stages of the oestrous cycle.

(*e*) *Pouch*

The pouch opens forward and in the mature non-parous female it is 60-80 mm in depth although it enlarges considerably in lactating females as the pouch embryo grows. The skin of the anterior of the pouch is well supplied with sebaceous glands and a viscous brown secretion is secreted at times but there is no apparent correlation between the stage of the cycle and pigment secretion. The pigment imparts a golden colour to the pouch fur and the fur around the mouth of the pouch. There are four nipples, the posterior two being directly behind and to the inside of the two anterior nipples.

IV. General Observations on Breeding

At birth the single embryo passes from the uterus to the exterior by way of the vaginal culs-de-sac, making a passage to the urogenital sinus and thus opening the pseudo-vaginal canal. A foetus taken from the pouch within 1 day of birth weighed 0.45 g; its mother's weight was 3120 g — approximately 7000 times that of the offspring. The length of this foetus from the nose to base of tail was 30 mm, the tail being 5 mm long. There is a well-developed phallus in both males and females at birth but neither scrotum nor pouch are distinguishable so that it is impossible to differentiate the two sexes. The newly born young has well-developed fore limbs whilst the hind limbs (which later in life far exceed the size of fore limbs) are rudimentary. The fore limbs are used by the young to climb into the pouch, apparently without aid from the mother. The young attaches to a single nipple, the mammary gland of which hypertrophies. During lactation this and no other nipple is used by the young. During the first week of pouch life the foetus does not tolerate examination and opening the pouch may cause premature death. At between a fortnight and 3 wk the embryo has attained a length of 40-60 mm and either pouch or scrotum can be distinguished. In the male the testes do not descend into the scrotum until approximately 8 wk after birth. From 2 wk onwards frequent examination and measurement of the pouch young do not harm it although removal from the nipple before the age of 12 wk usually results in death. At 12 wk the living pouch young weighs approximately 60 g and its length from nose to base of tail is approximately 15 cm around the curvature.

At 20 wk the pouch foetus exceeds 25 cm and 300 g. The eyes are open and it is lightly furred although it does not leave the pouch. At the age of about 25 wk the young leaves the pouch and is capable of swift movement although it will seek the pouch if it is alarmed. It is heavily furred, weighs approximately 600 g, and measures about 35 cm. Lactation continues during the following 3-4 months, the young feeding on the elongated nipple from the exterior after it becomes too large to enter the pouch. We have recorded several cases of females feeding one offspring from the exterior whilst another — very much younger — offspring occupies the pouch, feeding on another nipple.

Females in the departmental compounds become sexually mature at the age of about 18 months. At this time they weigh approx. 2 kg and their length from nose to base of tail is about 45 cm. The tail is only 25 cm, being very short compared with that of other macropod marsupials.

V. Acknowledgments

We wish to express our thanks to Mr. J. Jeapes for animal maintenance; to Mr. J. Stark, Secretary of the Rottnest Board of Control, for cooperation; to Mr. A. J. Fraser, Chief Warden of Fauna in Western Australia, for permits to collect this protected animal, and for assistance with transport. Figures 1, 2, and 3 were drawn by Mr. G. E. Binstead.

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EXPLANATION OF PLATE 1

All microphotos × 60 except 9 and 10 which are × 200.

Fig. 1.—Section of ovary with nearly mature Graafian follicle and egg.

Fig. 2.—Section of ovary with young corpus luteum. The centre contains only connective tissue and is not yet filled in with luteal cells.

Fig. 3.—Transverse section of lateral vagina. Note outer circular and inner longitudinal muscle layers and lining of stratified squamous epithelium.

Fig. 4.—Transverse section of median vaginal culs-de-sac. Note the remnants of the ruptured median septum.

Fig. 5.—Transverse section of median vaginal culs-de-sac in a non-parous animal. Note the presence of a complete median septum and the relatively large size (cf. Fig. 4). The animal is approaching oestrus, when marked hypertrophy of anterior culs-de-sac takes place.

Fig. 6.—Transverse section showing the opening of the pseudo-vaginal canal into the posterior vaginal sinus in a parous animal. Urethra above. Note that the pseudo-vaginal canal is, at its posterior end, lined with a single layer of columnar epithelium (cf. Figs. 4 and 5 at a more anterior position where a stratified squamous epithelium is present).

Fig. 7.—Transverse section of uteri with anterior vaginal expansion between.

Fig. 8.—Transverse section at lower end of median vaginal culs-de-sac in a non-parous animal (cf. Fig. 6).

Fig. 9.—The stratified squamous epithelium of median vaginal culs-de-sac at an anterior position.

Fig. 10.—The epithelium of median vaginal culs-de-sac at a position posterior to that of Figure 9. Note the transition from stratified squamous epithelium (at right) to a single layer of columnar cells (at left).

STUDIES ON MARSUPIAL REPRODUCTION

II. THE OESTROUS CYCLE OF SETONIX BRACHYURUS

By G. B. Sharman*

(*Manuscript received June* 16, 1954)

Summary

Setonix brachyurus Quoy and Gaimard is polyoestrous, the length of the cycle being about 28 days. In the wild and in the newly domesticated female, oestrous cycles are resumed in late January after an anoestrous period of 3-5 months. During this period oestrus does not occur and ovary and uterus are shrunken and quiescent. Domestication for periods exceeding 1 yr results in a greatly shortened anoestrous period, culminating in a condition in which oestrus is repeated at regular monthly intervals throughout the year.

Pro-oestrus is accompanied by rapid growth of one Graafian follicle, mitotic activity in the uterus, and usually by the onset of cornification in the vaginae and appearance of partly cornified cells in the smear. At oestrus the largest follicle reaches a diameter of almost 3.0 mm. Behavioural oestrus lasts about 12 hr. Ovulation follows 12-24 hr after oestrus and is independent of the act of copulation. Invasion of the collapsed follicle by blood vessels and the growth of a corpus luteum takes place after ovulation. Under the influence of the corpus luteum a luteal phase occurs in the uterus and lasts until about 18 days after oestrus. During the period of activity of the corpus luteum the vaginal smear is almost entirely composed of non-cornified cells and leucocytes. Following the cessation of the luteal phase degenerative changes occur in the uterus and the uterine glands are invaded by leucocytes.

The changes during the oestrous cycle in *Setonix* are compared with those occurring in *Didelphis* and in other marsupials.

I. Introduction

In a previous paper (Waring *et al.* 1955) the anatomy and histology of the reproductive system of the Rottnest Island wallaby (*Setonix brachyurus* Quoy and Gaimard) were described. Preliminary observations on breeding and the general techniques of histology, surgery, animal husbandry, etc., were treated in the earlier paper. The present paper is a description of the cyclic changes taking place in the reproductive system of the non-fertilized female *Setonix*.

II. Material

Fifty females have been studied. The reproductive systems of 20 of these were sectioned and stained for histological study.

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III. CYCLIC CHANGES IN THE REPRODUCTIVE SYSTEM OF THE UNFERTILIZED FEMALE

(*a*) *Anoestrus*

(i) *Occurrence.*—In the wild population on Rottnest I. we have observed an anoestrous phase in representative series of females taken during November, December, and early January in 1952 and 1953. The exact time of the onset of anoestrus in the wild population is unknown, although we have verified the occurrence of sexual receptivity in wild animals during July and have recorded births in late August. Probably anoestrus begins in the wild during August. Normal oestrous cycles are resumed in late January or early February and most births occur during February and March after a gestation period of about 27 days. At the time of a preliminary communication (Sharman 1954) it was believed that the beginning of anoestrus was coincidental in wild and domestic populations. Further work has shown that, although newly captured females exhibit an anoestrous period of comparable length to that of the wild female, continued domestication leads to a greatly shortened anoestrous period in the second year of captivity. In some long-domesticated females we have found oestrus to be repeated at monthly intervals throughout the year without intervention of an anoestrous period. The exteroreceptive stimuli determining anoestrus are unknown, although probably a combination of factors such as diet, length of day, etc. are responsible. Presumably the occurrence of a long anoestrous period in the newly domesticated animal is due to an impressed rhythm carried over from the wild state being thereafter suppressed by the changed environment of captivity.

(ii) *Ovaries.*—During anoestrus these are small in size without mature Graafian follicles or recent corpora lutea. Degenerate old corpora lutea averaging 1.3 mm in diameter are, however, found. These remain as scar tissue remnants for very long periods, and probably never entirely disappear during the life of the animal. The ovary is not entirely quiescent during anoestrus, because occasional mitoses are found in the granulosa cells of the follicles.

(iii) *Uteri.*—The two uteri are small in size and pale in colour. Glands are few and poorly developed (Plate 2, Fig. 16) and the uterine epithelium resembles that of the castrated or immature animal. No mitoses occur in the lumen or gland epithelia. During anoestrus the uterus is clearly distinguishable, both macroscopically and microscopically, from the uterus of an animal at any stage of the oestrous cycle.

(iv) *Vaginae.*—The vaginal complex is lined throughout with a non-cornified stratified epithelium. Only a meagre smear consisting of a few nucleated epithelial cells can be obtained.

(b) *Pro-oestrus*

(i) *Ovaries*.—Rapid growth occurs in one follicle and mitoses are common in the granulosa cells. In the first pro-oestrus following anoestrus only small and degenerate corpora lutea are found. During the second and following oestrous cycles, however, the corpus luteum of the preceding ovulation is prominent in one ovary at pro-oestrus. The luteal cells of this old corpus luteum are degenerative, as shown by their small diameter and the crumpled appearance of their nuclei. The size relationships of corpus luteum and follicle, in this and following phases of the cycle, are shown graphically in Figure 1.

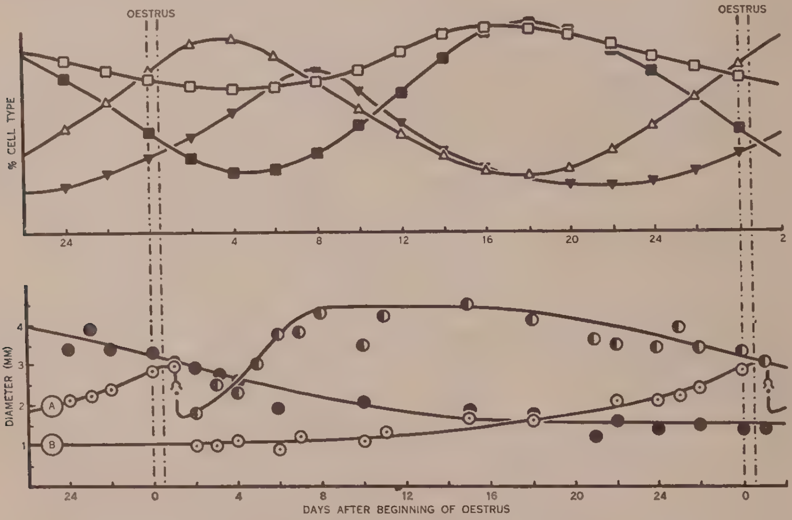

Fig. 1.—Above. Cyclic changes in the vaginal smear from living animals. □ Non-cornified epithelial cells. △ Partly cornified epithelial cells. ▼ Cornified (enucleate) cells. ■ Polymorphonuclear leucocytes. Below. Measurements of corpus luteum and follicle diameter in 18 animals killed at various stages of the oestrous cycle. ◉ Maturing follicles (*A* and *B*) of two successive ovulations. ◐ Corpora lutea of two successive cycles.

(ii) *Uteri*.—Externally the uteri are distinguishable from those of anoestrous animals by their greater diameter and a pinkish colour due to an increased vascular supply. Mitoses begin in the epithelial cells of uterine lumen and glands and the glands are enlarged and more numerous. Mitoses become increasingly common as oestrus approaches and the epithelial nuclei, especially in the lumen, become arranged in several layers. Blood vessels are commonly seen in sections of the uterus.

(iii) *Vaginae*.—The histological changes in the vaginal complex are variable. There is usually some degree of cornification of the lateral vaginal epithelium. This varies from slight, affecting only the inner layer or two of cells, to marked, when several cell layers are heavily cornified and enucleate. The median vagina and posterior vaginal sinus are non-cornified, although some changes foreshadowing oestrus can be seen in the latter (Plate 2, Fig. 14). Typically the lumen of the anterior vaginal culs-de-sac becomes enlarged towards the end of pro-oestrus.

(iv) *Smear*.—This consists of non-cornified epithelial cells, partly cornified epithelial cells, cornified cells, and polymorphonuclear leucocytes. The partly cornified cells are distinguished by a smaller more deeply staining nucleus than that of the non-cornified cell. The nucleus of the partly cornified cell is usually irregular in outline, and the cell itself may be somewhat flattened and irregular. Pro-oestrus is typically associated with a rise in the proportions of cornified and partly cornified elements in the smear, coupled with a fall in the proportion of leucocytes. In some cases, however, cornified cells do not appear in the smear until oestrus or slightly later. This is due to the delayed onset of cornification in the lateral vagina.

Inspection of Figure 1 shows that no cell type is ever completely absent from the smear. This is presumably due to some cells being held for long periods after sloughing off in the small canals of the reproductive system and contributing to the smears days, or even weeks, later. In general, changes in the smears lag behind the actual changes in the ovary and uterus which they indicate. This is hardly surprising when it is remembered that the smears are taken from the posterior lateral vaginal region. The more anterior part of the lateral vagina is never reached when the smear is taken so that cells from here — the most heavily cornified region — must be sloughed off and drift down before being collected.

(*c*) *Oestrus and Ovulation*

(i) *External Changes*.—At oestrus the phallus may protrude slightly and present a slightly reddened appearance. Neither of these are, however, reliable criteria for the diagnosis of oestrus. No changes in the size of the mammary glands, such as described by Hartman (1923) for *Didelphis*, are discernible at oestrus in *Setonix*. The most constant macroscopic change associated with oestrus is the relaxation and slight enlargement of the urogenital sinus. This makes the taking of vaginal smears less difficult, and is at once obvious during smearing.

The duration of oestrus, as defined by the time during which the female will accept a male for copulation, is rather short — almost certainly not longer than 12 hr. During this time the female will accept a series of males or the same male repeatedly. In the presence of an oestrous female males become excited, standing on their hind legs, at the same time sweeping the tail rapidly from side to side over the ground. When several males are present severe fighting may occur between them as each attempts to copulate with the female. Only on rare occasions does the male attempt to mate with the non-oestrous female and at such times is rejected. The occurrence of copulation can be verified by smearing up to 24 hr after the act. Since sterile copulation in no way affects the histological changes following oestrus, nor the time of the following oestrus, receptivity can be accurately diagnosed by mating with a vasectomized male. The appearance of prostatic bodies in the smear then indicates that oestrus and mating have occurred.

(ii) *Ovaries.*—At oestrus the single large Graafian follicle has attained a diameter of about 2.8 mm and the first maturation division is proceeding (Plate 1, Fig. 1). Mitoses are very common in the granulosa cells. The corpus luteum of the preceding ovulation is still large and exceeds the diameter of the mature follicle. Marked degenerative changes are, however, found in its luteal cells (Plate 2, Fig. 15). Ovulation occurs between 12 and 24 hr after the beginning of behavioural oestrus; the follicle reaching a diameter of almost 3 mm just before collapse. Ovulation is entirely independent of the stimulus of copulation and occurs in unmated as well as in mated animals.

(iii) *Uteri.*—These show a continuation of the pro-oestrus mitotic activity (Plate 1, Fig. 2). The nuclei of the epithelia are regularly oval in shape and their nucleoli prominent. Cilia are usually discernible on both lumen and gland epithelia. These occur on groups of cells interspersed at intervals throughout the epithelia.

(iv) *Vaginae.*—The lateral vaginae are variably — usually heavily — cornified. At this stage the posterior vaginal sinus may show slight cornification of the outer layers of epithelium coupled with changes, probably of a degenerative nature, in the cell nuclei. These cells make up, in some part, the increasing numbers of partly cornified cells found in the smear (Plate 1, Fig. 8). The lumen of the anterior vaginal culs-de-sac is greatly enlarged, but the epithelium remains non-cornified as at all other stages of the cycle (Plate 1, Fig. 7).

(*d*) *Days* 2 *to* 6 *after Oestrus*

This stage is the period of growth of the corpus luteum and of the initiation of correlated changes in the uteri. These changes will be subsequently referred to as luteal.*

(i) *Ovaries.*—Ovulation is followed by rapid invasion of the collapsed follicle with blood vessels (in which many mitoses occur) from the theca interna. The granulosa cells, with the exception of the cumulus oophoricus, are retained in the follicle and become the luteal cells of the corpus luteum. The developing corpus luteum is also invaded by cells from the theca interna. Mitoses have been observed in the luteal cells of the developing corpus luteum as late as three days after ovulation (Plate 1, Fig. 3). It is not known whether these mitoses occur in the luteal cells derived from the granulosa or in those derived from the theca interna cells. Probably they occur in both. The luteal cells derived from the theca interna (theca luteal cells) probably remain smaller than those derived from the granulosa cells. As in the pig (Corner 1921) there is no evidence that the theca interna cells are converted to fibroblasts. Hypertrophy of the luteal cells becomes marked on days 3 and 4 after ovulation and the corpus luteum rapidly attains large size. Growth appears to be complete by about 6 days after oestrus (5 days after ovulation) when the diameter is approx. 4 mm.

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* Unpublished work by Sharman and Waring has shown that injections of progesterone into ovariectomized animals evoke the changes here designated luteal. These changes, to be described later in this paper, are not as pronounced as in the rabbit where the uterine glands branch in a typical manner and assume a fern-like appearance under the influence of progesterone.

The passage of the unfertilized egg down the oviduct is exceedingly rapid. As in *Didelphis* (Hartman 1923) the egg reaches the uterus about 1 day after ovulation. Two days after ovulation, in the unmated female, the degenerating egg is found far down the uterus.

(ii) *Uteri.*—The uteri probably hypertrophy after oestrus and ovulation. Direct external measurements are, however, of little value, with small numbers, because of the large size variation in uteri from different animals. Mitoses are common in lumen and gland epithelia during the 2-3 days following oestrus but cease thereafter. Cessation of mitotic activity is followed by luteal changes in the uteri. The time of onset of these changes is variable but they are usually in evidence 5-6 days after oestrus. Luteal changes are first evident in the outer glands of the uterus but gradually spread inwards. The affected glands assume a larger size and greater epithelial cell height. The nuclei are circular in cross section and located basally in the cells (Plate 1, Fig. 4). The cytoplasm is chromophobic in contrast to its acidophilic nature at earlier stages of the cycle.

(iii) *Vaginae.*—The lateral vaginae are heavily cornified (Plate 1, Fig. 5) and sloughing off of cornified cells is marked on the second day after oestrus. In the posterior vaginal sinus and anterior urogenital sinus sloughing off also occurs although the sloughed off cells are at most partly cornified. This leads to one of the most characteristic and regularly recurring changes in the cycle: the posterior vaginal sinus becomes occluded with a dense mass of sloughed off matter (Plate 1, Fig. 6) which is recognizable without the use of a microscope. This usually occurs in its greatest mass 4 days after oestrus and may last several days. The observed recurrence of this phase at 28-day intervals provided the first evidence of a polyoestrous condition in *Setonix*. Sloughing off is followed by the return of a non-cornified condition throughout the vaginal complex (Plate 2, Fig. 17). The anterior vaginal culs-de-sac return to normal size soon after oestrus.

(iv) *Smear.*—The smear consists of profuse numbers of partly cornified cells, completely cornified cells, and epithelial cells (Plate 1, Fig. 9). Few leucocytes occur.

(*e*) *Days* 7 *to* 18 *after Oestrus*

This is the period of maximum size of the active corpus luteum, and a continuation of the luteal phase in the uterus.

(i) *Ovaries.*—The luteal cells are large with rounded nuclei containing prominent intensely basophilic nucleoli (Plate 2, Fig. 10). About 18 days after oestrus some degenerative changes begin in the luteal cells. These are at first evident only as a slight loss of regularity in the outline of the nuclear membrane and a loss of basophily of the nucleoli. Regression in overall size is not evident until later in the cycle. Towards the end of the active phase of the corpus luteum one follicle is usually of greater diameter than the remainder. Thus the largest follicle may be nearly 2 mm in diameter by the 18th day after oestrus. This — the maturing follicle of the ensuing ovulation — is usually located in the ovary not occupied by the functional corpus luteum.

(ii) *Uteri.*—During this period little change occurs in the size of the uterus. At first the luteal nature of the glands becomes more evident and the changes spread inwards until in the extreme case all the glands and the uterine lumen are affected (Plate 2, Fig. 11). Typically, however, the innermost glands and the lumen do not become luteal in nature. Ciliation of the epithelium is not as noticeable as during the two preceding phases. No mitoses occur.

(iii) *Vaginae.*—The vaginal complex is non-cornified throughout.

(iv) *Smear.*—The smear consists almost entirely of leucocytes and epithelial cells, only a few cornified elements being found.

(*f*) *Days* 19 *to* 23 *after Oestrus*

(i) *Ovaries.*—The corpus luteum becomes smaller in diameter and degenerative changes are evident in the luteal cells (Plate 2, Fig. 12). The follicle of the ensuing ovulation has a diameter of about 2 mm.

(ii) *Uteri.*—Coincident with the degeneration of the corpus luteum changes of a degenerative nature are found in the uterus. These are first evident by a lower epithelial cell height and a resumption of an oval shape by the nuclei. The nucleoli are no longer as distinct or as basophilic as during the period of the active corpus luteum. Some glands are invaded by polymorphonuclear leucocytes which migrate through the epithelium and become lodged in the gland cavity (Plate 2, Fig. 13). At about the 23rd day after oestrus a few mitoses may occur in the epithelia. Cilia are not obvious.

(iii) *Vaginae.*—These are typically non-cornified although the inner layers of the lateral vaginal epithelium usually show slight changes foreshadowing their future cornification.

(iv) *Smear.*—The smear continues to exhibit mainly non-cornified cells and leucocytes with a slightly greater incidence of partly cornified cells towards the close of the phase.

IV. Number of Oestrous Cycles per Year

The histological and anatomical changes described above are repeated in the non-fertilized female at intervals averaging 28 days. Animals in the wild have an anoestrous period (Section III(*a*)) starting approximately in August and terminating in late January or early February. Animals in their first year of domestication behave similarly. Those domesticated for 2 yr or longer apparently have continual oestrous cycles throughout the year. However, females born in our pens, from mothers not exhibiting the annual anoestrus due to long domestication, are exceptions. In such animals oestrous cycles commence at the age of 18 months (Waring *et al.* 1955) and the number of ovulations which have occurred during any subsequent period can be determined by counting the residual scar tissue of degenerated corpora lutea. In two animals the number of corpora lutea counted were too few, indicating that an anoestrous period had occurred at some time. The ovaries of three 2-yr-old females killed during the summer months were examined. All were in anoestrus although remnants of degenerated corpora lutea indicated that two to four oestrous cycles had occurred before the onset of anoestrus. Thus these animals, derived from parents whose annual anoestrus has been eliminated, show a reversion to wild type conditions in their first breeding year although subsequently exhibiting a continuous breeding season. The causative agents of the anoestrus in the wild are not fully investigated. It is, however, remarkable that animals, born under conditions where their mothers have ceased to show an annual anoestrous phase, have what appears to be an impressed rhythm forcing an anoestrous period (which is subsequently lost) upon them.

Since most or all wild females become pregnant, ovulation being withheld during subsequent lactation, it is not possible to determine the length of the reproductive phase in wild animals by counting corpora lutea. We have, however, examined a large series of reproductive systems from pregnant and lactating females taken in the wild. Several of these show recent degenerating corpora lutea in addition to those of pregnancy and lactation. This indicates that one or more cycles occurred before fertilization and shows a polyoestrous condition to be the rule in wild as well as domestic animals. Further confirmation has been obtained from lactating females taken in the wild and transferred to the department; those which lose their pouch young during transit later show a recurrence of oestrus.

V. Discussion

In an earlier paper (Waring *et al.* 1955) attention was drawn to the paucity of present knowledge on marsupial reproduction. Much is of course known of reproduction in the American opossum *Didelphis* (Hartman 1923; Reynolds 1952). In its basic essentials the cycle of *Setonix* shows great similarity to that of this primitive polyprotodont. Duration and number of oestrous cycles per year and the length of the anoestrous period appear comparable in both animals. As regards the remaining Australian species only two significant papers need be discussed. These are Hill and O'Donoghue's (1913) paper on the polyprotodont *Dasyurus* and Flynn's (1930) paper on the diprotodont *Bettongia.*

Some comment on the terminology used by earlier workers on marsupial reproduction is perhaps necessary so that valid comparisons can be made between this description and previously published work. In this paper the terms are restricted to anoestrus, pro-oestrus, and oestrus; the changes immediately following oestrus being defined only in terms of their duration. Perusal of the literature indicates that some terms describing phases of the oestrous cycle have not been used consistently. There seems little doubt on what is meant by anoestrus, pro-oestrus, and oestrus, but there appears to be confusion in the use of the terms metoestrus and pseudo-pregnancy. Following oestrus and ovulation it is customary to refer to the ensuing correlated changes in the uterus and vagina as constituting metoestrus. No doubt this term is properly applicable to the rat and mouse which now seem to be foremost in people's minds as standard. As defined by Heape (1900) metoestrus is a period of regression in the uterus and vagina and it is implicit in this statement that there is at this time no functional corpus luteum. In those forms in which there is a functional corpus luteum whether there has been copulation or not, it has become customary to refer to this phase (following Hill and O'Donoghue's original usage) as pseudo-pregnancy. The objection to the use of this term in the absence of copulation needs no emphasis. In *Setonix* ovulation is always followed by a functional corpus luteum and the uterus bears histological evidence of a change mediated by progesterone. This could be referred to as pseudo-pregnancy, but the objection to this has been indicated. It would be definitely misleading to refer to it as metoestrus. The only alternative seems to be to follow the example of Corner (1921) defining the phases, as he did in the sow, by the number of days after a valid marker in the cycle (i.e. after oestrus). We consider that the term pseudo-pregnancy is best applied to such animals as the rat where sterile copulation is followed by progestational changes in the uterus, resulting from luteal action, which do not occur in the unmated female.

Some limited comparison of the results obtained during this study with those of earlier workers on Australian marsupials is possible. Flynn's (1930) study of the diprotodont *Bettongia* unfortunately suffers from the lack of controlled observations on animals breeding in captivity so that accurate data on the length of the oestrous cycle in this animal are therefore not available. Since the females studied by Flynn were pregnant, and taken from the wild, no information is available on the changes following ovulation in the non-fertilized animal. *Bettongia,* however, like *Setonix,* bears but a single young and Flynn has demonstrated changes in the non-pregnant uterus strictly comparable with those occurring after ovulation in the non-fertilized *Setonix*. *Bettongia* (again like *Setonix*) is polyoestrous and Flynn believed that an anoestrous period occurs during the summer months. The occurrence of an anoestrous period during the summer months in the only two macropod marsupials that have been intensively studied is therefore of considerable interest when it is remembered that anoestrus in many northern hemisphere eutherians (and in *Didelphis*) occurs in the winter months.

Hill and O'Donoghue's (1913) paper predated Hartman's (1923) studies on *Didelphis* and much of the earlier work on the oestrous cycles of eutherians. At this time the technique of vaginal smearing as an index of the cyclic changes taking place during reproductive processes was unknown. These authors considered *Dasyurus* to be monoestrous although one of them (Hill 1919) later expressed doubts as to the validity of this finding. As the observations on *Dasyurus*, and the collection of the material, appear to have been limited to only part of the year we do not consider that sufficient evidence has been amassed to make a firm decision as to whether one or more oestrous cycles occur in the unfertilized female during one year. As far as comparisons are possible the changes associated with oestrus and ovulation, and the changes following ovulation, appear strictly comparable in *Dasyurus* and *Didelphis*.

Certain similarities are evident in the reproductive processes of the four marsupial species so far studied. *Didelphis, Setonix,* and *Bettongia* are polyoestrous, and in the first two animals the length of the oestrous cycle is approx. 28 days. *Dasyurus* is considered monoestrous, although the evidence on this matter is not conclusive. In all four marsupials ovulation is followed by changes in the uteri correlated with an active corpus luteum; and since these changes are mimicked by injections of progesterone in *Setonix* and *Didelphis* we are entitled to call them luteal. In *Didelphis, Dasyurus,* and *Setonix* these occur in the non-mated animal following spontaneous ovulation. In *Bettongia* the same probably occurs, although appropriate animals have not been studied. However, certain basic differences in reproductive processes between the diprotodont and polyprotodont forms, especially with regard to gestation, are demonstrable. These will be discussed fully in a following paper.

VI. Acknowledgments

This research has been conducted with the aid of grants from several sources. Financial assistance from the C.S.I.R.O. Science and Industry Endowment Fund, Commonwealth Research Grants, and especially the Nuffield Foundation, which paid salary and expenses for the author, is gratefully acknowledged.

The *Setonix* domestic colony has been maintained by Mr. J. Jeapes and technical assistance has been given by Miss J. Nathan. Mr. A. J. Fraser, Chief Warden of Fauna in Western Australia, has permitted the taking of specimens from Rottnest I. and has also helped with transport.

Mr. J. Stark, Secretary to the Rottnest Board of Control, has been cooperative and helpful at all times.

The work has been supervised by Professor H. Waring, to whom I am deeply indebted for help in the field, and for careful reading and criticism of the manuscript.

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Explanation of Plates 1 and 2

Plate 1

All photographs × 115.

Fig. 1.—Follicular ovum 1 day after oestrus, showing chromosomes of first polar body, cumulus, and granulosa cells.

Fig. 2.—Portion of uterus, showing lumen epithelium and uterine glands, slightly after oestrus. Note mitoses in epithelium *and that nuclei are not restricted to basal layer* (cf. Plate 2, Fig. 11).

Fig. 3.—Cells of new corpus luteum 3 days after oestrus, showing mitosis in luteal cell (at centre).

Fig. 4.—Beginning of luteal changes in uterus 5 days after oestrus. The outer glands (at right) show a greater cell height than those nearer the lumen (at left bottom corner). Note the difference in the staining reaction betwen cytoplasm of outer and inner epithelia.

Fig. 5.—Heavily cornified epithelium of lateral vagina 4 days after oestrus.

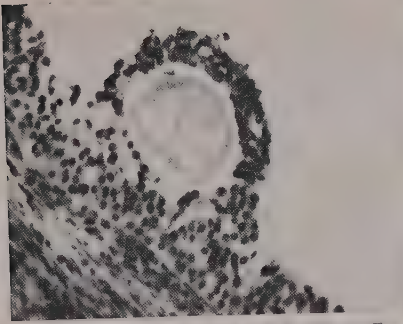
Fig. 6.—Epithelium and contents of posterior vaginal sinus 4 days after oestrus. Note sloughing off of partially cornified cells from epithelium and collection of sloughed off cells from this and other regions of the vaginal complex.

Fig. 7.—Non-cornified epithelium of the median vaginal cul-de-sac at approximately the same stage of the cycle as in Figures 5 and 6.

Fig. 8.—Some cells from the smear of an animal at oestrus. These cells, in which the nucleus is small and densely stained and the outline somewhat irregular, are designated as partly cornified in the description of the smears. Their appearance in the smear usually foreshadows the approach of oestrus.

Fig. 9.—Some cells from the smear of an animal 4 days after oestrus. Not all elements found are shown in the field of this photograph. Note the profuse numbers of cells, most of which are partially cornified but still nucleate.

STUDIES ON MARSUPIAL REPRODUCTION. II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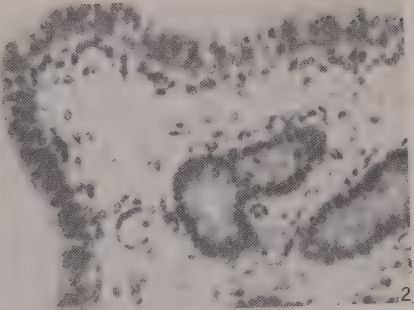
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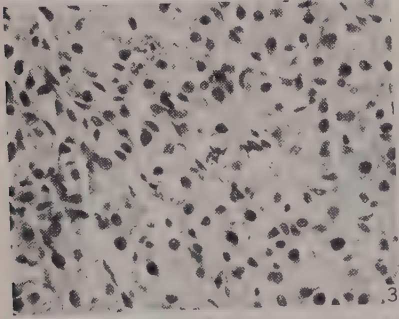
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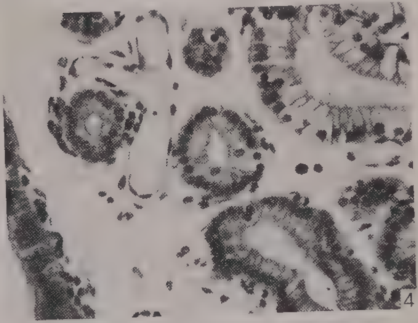
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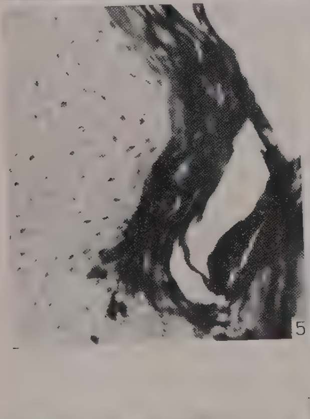
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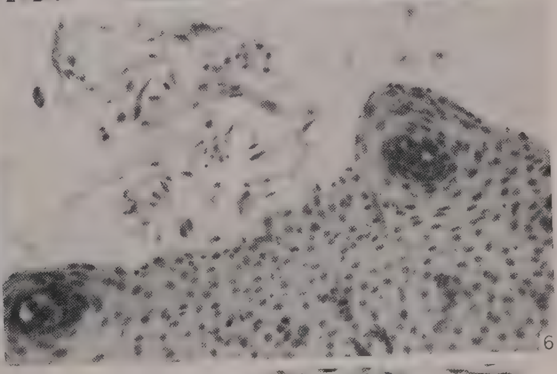
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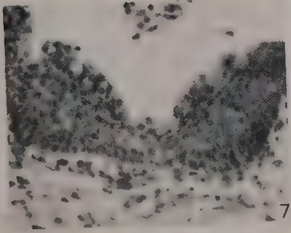
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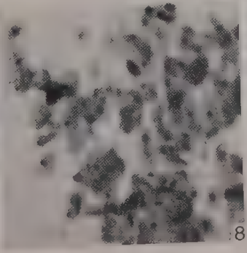
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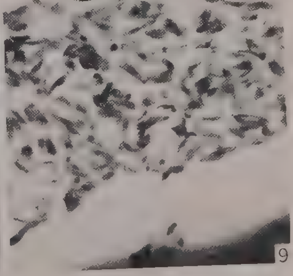
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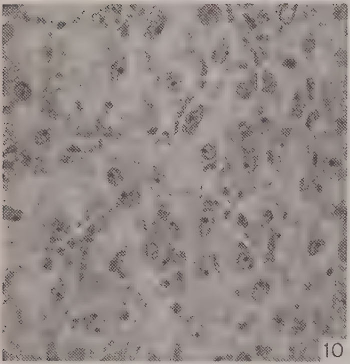
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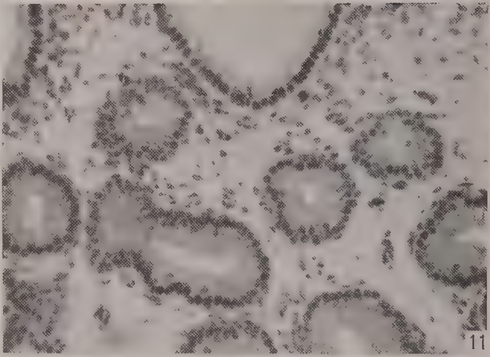
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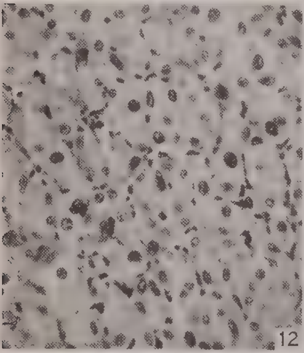
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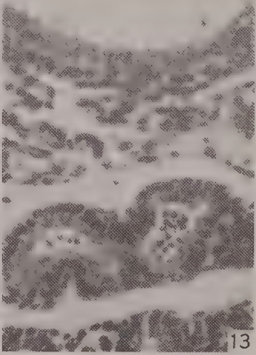
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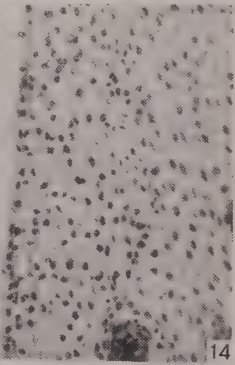
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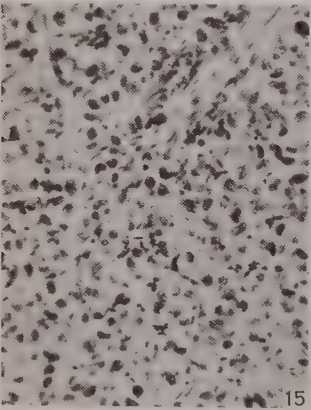
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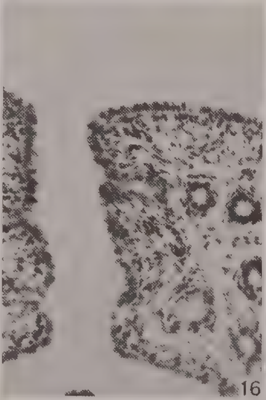
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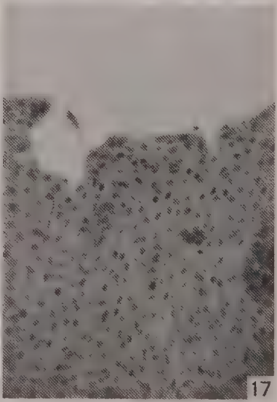
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PLATE 2

All photographs × 115.

Fig. 10.—Cells from a mature corpus luteum 8 days after oestrus. Note large cell size and strongly basophilic nucleoli.

Fig. 11.—Gland and lumen epithelium (at top), in an animal 8 days after oestrus, showing marked luteal changes. Note *basal position of the gland nuclei*, great cell height, and non-staining cell cytoplasm (cf. Figs. 2, 4, and 13).

Fig. 12.—Cells of a degenerating corpus luteum 24 days after oestrus. Note smaller cell size (cf. Fig. 10) and irregularity of nuclear outline.

Fig. 13.—Invasion of uterine glands by leucocyctes 24 days after oestrus.

Fig. 14.—Epithelium of posterior vaginal sinus 26 days after oestrus. The approach of the following oestrus is foreshadowed in the nature of the epithelial cells which are vacuolate with strongly basophilic and irregular nuclei.

Fig. 15.—Cells of old degenerating corpus luteum at time of following oestrus (cf. Figs. 10 and 12).

Fig. 16.—Lumen and glands in uterus of an animal in anoestrus. Note small size of glands and poorly developed epithelia.

Fig. 17.—Lateral vaginal epithelium of an animal 8 days after oestrus. Note the absence of cornification (cf. Plate 1, Fig. 5).

STUDIES ON MARSUPIAL REPRODUCTION

III. NORMAL AND DELAYED PREGNANCY IN SETONIX BRACHYURUS

By G. B. Sharman*

(*Manuscript received June* 16, 1954)

Summary

The period between copulation and birth in *Setonix brachyurus* Quoy and Gaimard is about 27 days. Approximately 1 day elapses between copulation and fertilization. The gestation period is slightly less than the length of one oestrous cycle.

The tubal journey of the fertilized egg occupies only about 1 day. The unilaminar blastocyst 3-4 days after mating, with its enclosing membranes, measures about 0.3 mm diameter. At this stage the corpus luteum is not fully developed and a luteal phase is not evident in the uteri. Bilaminar blastocysts and later embryonic stages are associated with a well-developed corpus luteum and luteal changes in the uteri. Towards the end of pregnancy the corpus luteum shows degenerative changes and ovaries and uteri exhibit evidence of approaching oestrus. The allantois of the uterine embryo does not form a placental structure. A well-developed, vascular, trilaminar yolk-sac placenta occurs during the later stages of embryonic life.

Oestrus and ovulation occur shortly after the female gives birth. The corpus luteum formed following post-partum ovulation remains of small size and functions during lactation of the young in the pouch as the corpus luteum of lactation. Luteal changes do not occur in the uterus during this time and a lactation anoestrus takes place. Removal of the young from the pouch causes growth of the corpus luteum of lactation and the onset of luteal changes in the uterus.

If fertilization takes place at post-partum oestrus the resulting embryo remains as an unimplanted blastocyst of small size during the time the pouch is occupied by a suckling foetus. This quiescent embryonic stage will proceed to normal development following removal of the young from the pouch. Blastocysts may remain unimplanted for up to 5 months.

The probable significance of the gestation period in relationship to the length of the oestrous cycle and the placental structure is discussed. The ovulation-inhibiting function of the corpus luteum of lactation and its later luteal function are compared. The mechanism of delayed pregnancy in *Setonix* is discussed and comparisons are made with known cases of delayed birth in other mammals. Some concluding remarks are made on the breeding habits of *Setonix* in relation to its environment.

I. Introduction

The changes associated with the oestrous cycle in the primitive polyprotodont marsupial *Didelphis* have been compared with those in the diprotodont wallaby *Setonix brachyurus* Quoy and Gaimard (the quokka). Both are polyoestrous and in each case ovulation, in the absence of copulation, is followed by a pronounced luteal phase in the uterus (Sharman

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1955). In *Setonix*, as in *Didelphis*, the length of the oestrous cycle is approx. 1 month. Apart from the number of ova maturing at oestrus (*Setonix* is exclusively monovular) no fundamental differences are apparent in the reproductive processes of unmated animals.

With regard to pregnancy, previous records (Kenneth 1947) indicate that gestation periods in diprotodonts greatly exceed that of *Didelphis*, but the evidence on which these records are based is insufficient. In *Didelphis* the gestation period is approximately half the length of a normal oestrous cycle, whereas in polyoestrous Eutheria gestation occupies the span of several oestrous cycles. Until now it has not been possible to decide whether any diprotodont resembles *Didelphis* in this respect. It is one object of this paper to record this information about normal pregnancy in *Setonix*.

Interest in the reproductive processes in diprotodont marsupials has been aroused by previous reports (Wood Jones 1924, 1944) of females in captivity giving birth to young at long periods after isolation from males. It is convenient to refer to this as delayed birth. Early in the present investigation it was found that female *Setonix* exhibited delayed birth after young being suckled had been lost from the pouch. Two possible explanations present themselves:

1. Spermatozoa may be stored for long periods in the female reproductive system before fertilizing the egg.
2. Marsupials may exhibit delayed implantation, as do lactating rats where females suckling large litters have a quiescent blastocyst stage of up to 19 days (Weichert 1942*a*).

In this paper the mechanism of delayed birth in *Setonix* is described.

II. METHODS

Approximately 40 females of *S. brachyurus* Quoy and Gaimard have been used for this study. Animals of known case histories were drawn from the departmental colony and the study of these supplemented with animals from the wild.

Gestation periods were determined from animals in which copulation was observed or verified by the occurrence of live spermatozoa in the vaginal smear, or both. After copulation had been verified the pouch was examined to rule out the possibility of confusion with post-partum oestrus, at which females also copulate. The pouch was thereafter examined every 1 or 2 days until birth occurred.

The following series of experiments were designed in order to elicit the mechanism of delayed birth:

(1) Serial sections were made of uteri of lactating females in order to locate the quiescent blastocyst. Blastocysts were also isolated by cutting off the uterus at its extremities, attaching a syringe of saline at the posterior end, and forcing the blastocyst out into a watch-glass.

(2) Females suckling pouch young were separated from males for a period equal to normal gestation or longer. The young were then removed from the pouches. After varying periods the females were killed and the uteri examined for the presence of developing embryos. Control animals which had been separated from males during post-partum oestrus were treated in the same way.'

(3) In order to test the possibility of delayed birth being due to the storage of spermatozoa the oviducts of anaesthetized females were tied and cut above the uteri. The pouch young were then removed and the uteri were later examined for developing embryos. If spermatozoa were stored in the reproductive system pregnancy could not ensue after the oviducts were destroyed as the egg of a new ovulation could not then be fertilized.

Histological techniques and the methods of taking vaginal smears are as previously described (Waring *et al.* 1955).

III. PREGNANCY

(*a*) *The Gestation Period*

Observations on the length of gestation have been made in females in which insemination was verified by the presence of live spermatozoa in the vaginal smear. Two of these when examined the 25th day after mating had not given birth. However, on the 27th day after mating both had young in the pouch. The third female gave birth on the 27th-28th day after mating. A fourth female placed with a male when in oestrus, but in which copulation was not observed, was found at autopsy 26 days later to have an embryo in the vaginal culs-de-sac in the process of birth. The period between copulation and birth is then about 27 days. Of this period approx. 1 day elapses between copulation and fertilization. As the length of a normal oestrous cycle is 28 days (Sharman 1955) the length of gestation in *Setonix* is slightly less than the length of one oestrous cycle. In *Didelphis* pregnancy lasts about half the length of one oestrous cycle (Hartman 1923).

Since pregnancy is shorter than a normal oestrous cycle, and the vaginal smear follows the same course as in a non-pregnant animal it can, as far as we know, only be diagnosed by examination of the uteri. From about the first week onwards the uterus containing the developing embryo becomes greatly enlarged, the non-pregnant uterus remaining of normal size.

(*b*) *Changes During Gestation*

(i) *The Fertilized Tubal Egg.*—Two days after copulation the fertilized egg is found in the lower oviduct. In the single example studied male and female pronuclei are not yet fused. Numerous supernumerary spermatozoa are found embedded in the zona pellucida and tertiary ("albumen") membrane of the fertilized tubal egg. There is, however, no evidence of penetration into the vitellus of more than one sperm, which gives rise to the male pronucleus. Both pronuclei are large and of about equal size. The average of the various diameters of the non-spherical egg, including all membranes, is 140 μ. The tubal journey of the fertilized egg does not exceed 2 days, and probably occupies only 1 day, as with non-fertilized eggs (Sharman 1955). No cilia can be demonstrated in the oviduct at any phase. In the American opossum the tubal journey also occupies but 1 day and the oviducts are non-ciliated (Hartman 1923).

During the tubal egg stage, in both fertilized and non-mated females, the uterine epithelia have many mitoses. Luteal changes, as described by Sharman (1955) are not, as a rule, exhibited in the uterus until later. However, the animal, in which the tubal egg, described above, occurred, was unusual in that changes of a luteal nature had begun. In no other animal have we observed the beginning of this phase earlier than 4 days after oestrus.

The vaginal complex and vaginal smear in the fertilized animal 2 days after mating may show a few spermatozoa and prostatic bodies, otherwise they are typical of those of the non-fertilized animal 2 days post oestrus.

(ii) *The Unilaminar Blastocyst.*—Blastocysts approaching 0.3 mm diameter consist of about 70 cells, most of which constitute the trophoblastic ectoderm. The embryonic region of the blastocyst is very small. An eosinophilic membrane, which appears to consist of attenuated zona pellucida and tertiary elements, surrounds the blastocyst. In the serially sectioned uterus the blastocyst is located nearer the posterior than the anterior end.

The corpus luteum of the female in which the 0.3 mm blastocyst is found is comparable in size and structure with that of the non-fertilized female 3-4 days after oestrus. The beginnings of luteal changes, as described by Sharman (1955), are evident in both pregnant and non-pregnant uteri at this stage.

(iii) *The Bilaminar Blastocyst.*—The reproductive systems of two females, in which bilaminar blastocysts of 8 and 12 mm diameter were found, have been studied. In both blastocysts a two-layered yolk-sac consisting of ectoderm and endoderm can be distinguished. In *Setonix,* as in other marsupials (Boyd and Hamilton 1952), the amnion arises by fold formation at the edges of the embryonic area.

In the two females with bilaminar blastocysts the corpora lutea measured 4.5 and 3.5 mm diameter. Only small immature follicles were found in the ovaries. In both animals the pregnant and non-pregnant uteri were in the luteal phase. Ovaries, uteri, and vaginal complex show the condition found in the non-pregnant animal 5-10 days after oestrus.

(iv) *The Early Embryo.*—The single embryo studied at this stage measures 4 mm in direct length, not including the foetal membranes. The neural groove is still open along its entire length. At this stage a vascular trilaminar structure is developed in a broad band surrounding the yolk-sac and making contact with the maternal uterine wall, the epithelium of which is flattened but not penetrated. This is the chorio-vitelline (yolk-sac) placenta formed by the growth of mesoderm between the trophoblastic ectoderm and the endoderm of the yolk-sac.

The corpus luteum in the ovary on the same side as the uterus carrying the embryo measures approx. 4.0 mm in diameter. Histologically this corpus luteum closely resembles that of a non-pregnant animal at about the same period after oestrus, i.e. 16 days. The luteal cells are large with rounded nuclei containing prominent basophilic nucleoli. Both uteri show pronounced luteal changes in the gland epithelia.

(v) *The Advanced Embryo.*—An advanced embryo studied in a serially sectioned uterus measures 10 mm in direct length without foetal membranes. The yolk-sac placenta is well developed and lies in close contact with the uterine wall. The maternal structures are, however, not invaded by the placenta and the uterine epithelium, though flattened where contact is made with the placenta, is complete. Histologically the epithelia of both uterine lumen and glands are not different at this stage from those of a virgin animal 20 days after oestrus. Such gross differences as occur in the pregnant uterus can be attributed to distension by the embryo. The allantois is smooth-walled, without blood vessels, and, although large, lies embedded in the yolk sac. An embryo of slightly later stage dissected from the uterus shows the allantois as a smooth-walled sac enveloped by folds of the yolk-sac. In *Didelphis*, in rat kangaroos, and kangaroos the allantois does not reach the chorion. Consequently a chorio-allantoic placenta is not developed (Pearson 1947). In other marsupials, e.g. *Dasyurus*, the allantois may reach the chorion without forming placental structures. Only the Peramelidae among the marsupials develop a true chorio-allantoic placenta (Hill 1897; Flynn 1923). Although sufficient stages have not been studied to determine the exact relationships between allantois and chorion we have found no placental structure in *Setonix* in which the allantois takes part. In our most advanced embryo still in the uterus there is a heavily vasculated well-developed yolk-sac placenta, and the size and development indicate that the embryo will shortly leave the uterus. We therefore believe that no allantoic placenta is developed at any stage during the uterine life of the embryo *Setonix*.

Three females exhibiting stages of gestation later than the above were killed for study. In one of these the embryo appeared to be just leaving the uterus as the mother was killed. The other two (one of which had exhibited oestrus symptoms 26 days before) both had embryos in the upper median vaginal culs-de-sac in the process of birth.

All the five animals studied and reported under this subheading show pro-oestrus changes. The luteal cells of the corpora lutea are degenerative and an enlarging follicle is found in one or other ovary. The follicles range from 1.4 to 2.5 mm diameter; the largest being associated with the most advanced embryos. In females with the most advanced embryos mitotic activity has begun in lumen and gland epithelia. None of the uteri, either pregnant or non-pregnant, show a luteal phase; this means the luteal induced condition rapidly relapses. That of the female bearing the least advanced embryo has leucocytic infiltration of the glands and is comparable to the uterus of a non-fertilized female 20 days after oestrus.

As in the diprotodont *Bettongia* (Flynn 1930) the foetal membranes appear to be largely retained within the uterus after birth, where they undergo rapid degeneration.

Parturition is by way of the median vaginal culs-de-sac, the embryo making a passage (the pseudo-vaginal canal) to the urogenital sinus in the non-parous animal. After the first parturition this passage remains open for the remainder of the life of the animal (Waring *et al.* 1955). It has been noted (Sharman 1955) that the upper median vaginal culs-de-sac become enlarged at pro-oestrus. Since the female shows the pro-oestrus condition at parturition it is possible that this enlargement, occurring as a normal phase of the oestrous cycle, is a significant agent during parturition, allowing an easier passage of the foetus down the birth canal.

IV. Changes Following Birth

In the foregoing section it has been shown that the life of the corpus luteum is probably not extended during gestation and that the cyclic changes associated with a normal oestrous cycle continue during this period. Oestrus and ovulation follow shortly after parturition at the same time as they would be expected had the female not been pregnant. At post-partum oestrus, which usually occurs the day following birth, the female will copulate if placed with a male. The significance of this behaviour will be discussed in the following section on delayed pregnancy. The corpus luteum formed following post-partum ovulation becomes the corpus luteum of lactation,* whether the egg is fertilized or not. Its formation, and growth during the first 3-4 days after ovulation, are normal and strictly comparable with similar stages of the corpus luteum of pregnancy and of the normal cycle. The corpus luteum of lactation, however, differs from other corpora lutea in its arrested growth and long life. During the period in which the foetus is suckled in the pouch the diameter of the corpus luteum of lactation does not exceed 2.5 mm (Fig. 1) and histologically it remains similar to the 3-4-day corpus luteum of the normal cycle. Suckling of the young in the pouch extends over 4-6 months (Waring *et al.* 1955) and during this time the corpus luteum of lactation can always be found in one or other ovary. During this period the female undergoes a lactation anoestrus and ovulation does not occur. The uteri are small in diameter

* Although we call this the corpus luteum of lactation, since it is present during lactation of the young in the pouch, it is clear that, if a corpus luteum is necessary for the *initiation* of lactation, the corpus luteum of pregnancy must fulfil this role.

with few glands, which often appear straight when seen in cross section. This glandular condition otherwise occurs only in seasonal anoestrus where it is more pronounced. In pregnancy and in unfertilized females exhibiting ordinary phasic changes of the oestrous cycle the glands appear circular or slightly coiled in cross section. Following the emergence of the young from the pouch (or after its premature death) the corpus luteum enlarges in size and a luteal phase of the uterus, comparable to that of the normal cycle ensues (Figs. 1, 2). This is followed by degenerative changes in the corpus luteum, decline of the luteal phase, and then pro-oestrous changes culminating in another oestrus and ovulation. Although the sterile period which occurs whilst the young is suckled has been called a lactation anoestrus it only persists while the young is suckled wholly *in the pouch.* In departmental compounds several females have been observed to exhibit oestrus and again became pregnant immediately after emergence of a pouch foetus. Such females suckle the emerged young on an elongated nipple while the second foetus occupies the pouch, feeding on another nipple. In the wild population, however, anoestrus begins before the earliest pouch young have emerged. Pregnancy does not therefore again occur before the beginning of the next breeding season.

V. Mechanism of Delayed Birth

As stated above, parturition is followed immediately by a post-partum oestrus during which the female will copulate. From this copulation, having regard to the observation that pregnancy lasts 27 days and pouch life 4-6 months, one might expect a second foetus to appear in the pouch. But two foetuses of different ages are never found in the pouch at one time. So either the sperm introduced at post-partum heat is stored somewhere in the female tract, or after fertilization there is arrested development. Either of these events would explain the recurrent observation that female marsupials, isolated for long periods from males, occasionally give birth to young.

At first we adopted as a working hypothesis, Wood Jones's (1924) contention that delayed birth was due to the storage of spermatozoa by the female. This was abandoned when we obtained unequivocal histological evidence that post-partum copulation resulted in immediate fertilization. Furthermore, spermatozoa, although easily found in the female tract immediately after copulation, are hardly detectable 2 days later. None are found after more than a week. So we next investigated another alternative — that of arrested development. Uteri of lactating females which have copulated in post-partum heat show no enlargement in size and preliminary serial sections failed to reveal any quiescent embryonic stage.

In the first series of *experiments* to test whether delayed birth was due to the storage of an unimplanted blastocyst, females taken from the wild, which could reasonably be expected to have copulated in post-partum heat, were isolated from males for 1 month or more. Their pouch young were then removed and after varying intervals the females were killed. In each case the corpora lutea of lactation were greatly enlarged as in other females following the removal or emergence of pouch young. All had developing embryos of varying stages in one or other uterus, and microscopical examination showed a luteal phase in the uteri (Figs. 1, 2). Females in our pens definitely known to have been separated from males before birth of their young were treated similarly. None were pregnant although all showed enlarged corpora lutea of lactation, and a luteal phase in the uterus.

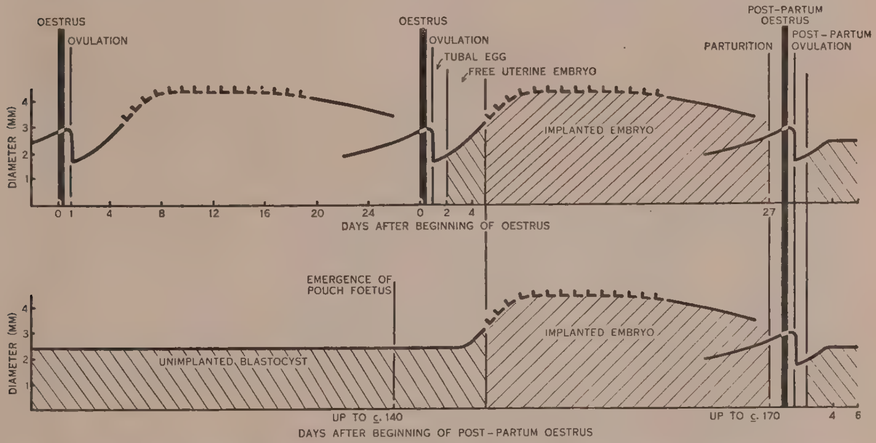


Fig. 1.—The size relationships of corpora lutea during the oestrous cycle (top left), gestation (right), and lactation with delayed implantation (bottom left) in *Setonix brachyurus*. The periods during which luteal changes are evident in the uterus are shown on the curves by the letters LL. Diagonal hatching sloping downwards to the right indicates unimplanted stages of pregnancy. Hatching sloping upwards to the right indicates implanted stages. For further explanation see text.

Two further lactating females with pouch young had their oviducts cut and tied above the uteri. The pouch young were removed from both. The first animal died 1 day after the operation and the uterus corresponding to the corpus luteum of lactation was flushed out with saline. A small blastocyst approximately 0.3 mm in diameter was recovered. The second female was found at autopsy 13 days later to have a large actively dividing bilaminar blastocyst in one uterus. In each case the oviducts were found to have been completely closed off by the operation, thus effectively ruling out the possibility of stored spermatozoa fertilizing the egg of an ovulation subsequent to the removal of the pouch young.

Serial sections of uteri of several more animals were subjected to thorough search; in two of these small blastocysts of less than 0.3 mm diameter were found in the uterus on the same side as the corpus luteum of lactation. Under similar circumstances blastocysts have since been recovered by flushing the uterus with saline. In its size and stage of development the stored blastocyst is comparable to the unilaminar blastocyst of normal pregnancy as described above.

The longest delayed birth accurately documented concerns a domesticated animal in which birth and post-partum copulation were verified and recorded. This female was then isolated from males until the foetus had left the pouch and was being fed on an elongated nipple from the exterior. Normal development of the stored blastocyst apparently began when the first young emerged, as a second new-born foetus was found in the pouch 171 days after post-partum copulation. The period of quiescence of the unimplanted blastocyst can then reach about 5 months. As in females resuming normal cycles after lactating young in the pouch, emergence of the pouch foetus and not cessation of lactation is sufficient stimulus to cause enlargement of the corpus luteum of lactation (Figs. 1, 2). Under the stimulus of the enlarging corpus luteum luteal changes begin in the uterus, thus preparing the endometrium for the reception of the blastocyst. After the delayed birth the usual post-partum heat occurs.

In the wild population on Rottnest I. we have found that females carrying a foetus in the pouch are also carrying a quiescent blastocyst. At the time of emergence of young from the pouch, however, the seasonal anoestrus has already begun. Conditions during anoestrus are apparently not suitable for development of the blastocyst and no females give birth to a second foetus while anoestrus continues. Blastocysts can no longer be demonstrated in the uteri of anoestrous females and it is believed that they degenerate at the beginning of this phase.

VI. DISCUSSION

In those eutherian mammals which exhibit a polyoestrous condition pregnancy occupies the span of at least several oestrous cycles. In both *Setonix* and *Didelphis,* the only marsupials for which relevant information is available, the length of gestation is exceeded by that of one oestrous cycle. These two marsupials differ only in that the gestation period of *Setonix* is approximately double that of *Didelphis,* although the length of the oestrous cycle of both is 28 days. Both have, until the termination of uterine life, a yolk-sac placenta. This type of placentation occurs only as a transitory phase in the embryonic life of some higher mammals. We have no information on the physiology of the yolk-sac placenta, although various workers have presented good evidence that the allantoic placenta secretes functionally useful oestrogenic, luteal, and gonadotrophic hormones during pregnancy (reviewed by Huggett and Hammond 1952). The luteal activity of the allantoic placenta is of particular significance to our theme. In the rat the 11-day pseudo-pregnancy without ovulation shows that the corpus luteum alone can be stimulated to secrete sufficient progesterone to inhibit ovulation. Equally clear is the evidence from experiments on removal of foetuses, and not their placentae (Newton 1935; Selye, Collip, and Thompson 1935), that in the second half of pregnancy the placentae maintain the ovarian corpora lutea sufficiently to inhibit ovulation. It is clear that, in *Setonix*, the act of copulation itself does not evoke sufficient activity in the ovarian corpus luteum to inhibit ovulation; with no allantoic placenta there exists no apparent method comparable to that of the eutherians for maintaining the life of the corpus luteum. Consequently delayed ovulation as a result of pregnancy would not be expected and in fact is not found. It is tempting to postulate that marsupials without an allantoic placenta may be physiologically incapable of inhibiting ovulation and therefore incapable of carrying an embryo in the uterus for periods exceeding one oestrous cycle. Unfortunately nothing is known of reproduction in the Peramelidae which, like the Eutheria, have allantoic placentation.

In *Didelphis* ovulation following birth does not occur and is withheld at the time of the next expected oestrus by the onset of a lactation anoestrous phase. At parturition in *Setonix* pro-oestrous changes are already initiated. The corpus luteum of pregnancy is degenerate and presumably cannot be stimulated by the suckling stimulus of the new-born young to inhibit ovulation. Oestrus and ovulation thus recur shortly after parturition at the time normally expected had pregnancy not occurred. Aside from its importance in connection with delayed birth, to be discussed later, post-parturition oestrus ensures that conception can occur immediately after birth. Bearing in mind the exceedingly undeveloped nature of the single offspring and the hazards of its journey to the pouch, the ability of the mother to become pregnant again at this time may be distinctly advantageous. If the young is lost normal pregnancy again takes place without further intervention of the male (Fig. 2).

The corpus luteum of pregnancy has the same length of life as in a virgin or non-mated female, and its secretions do not inhibit ovulation. By contrast the corpus luteum of lactation appears to definitely inhibit ovulation during the pouch life of the young (Fig. 1). It is noteworthy that even though it has this property it is small and histologically resembles the 3-4-day corpus luteum of the oestrous cycle. The precise endocrine relationships during lactation are difficult to interpret at present. The persistence of the corpus luteum, with its attendant lactation anoestrus, only continues while a foetus is suckled in the pouch. Emergence, with continuance of lactation externally, or premature death of the pouch foetus cause growth of the corpus luteum and the onset of luteal changes in the uterus (Figs. 1, 2). The simplest interpretation of these results is that when small the corpus luteum of lactation exerts only an ovulation-inhibiting effect, presumably under stimulus of lactation in the pouch. When, after removal of the foetus, the corpus luteum enlarges it also evokes luteal changes in the endometrium. These endometrial changes are, of course, appropriate for the reception of the blastocyst, the development of which is previously inhibited by lactation.

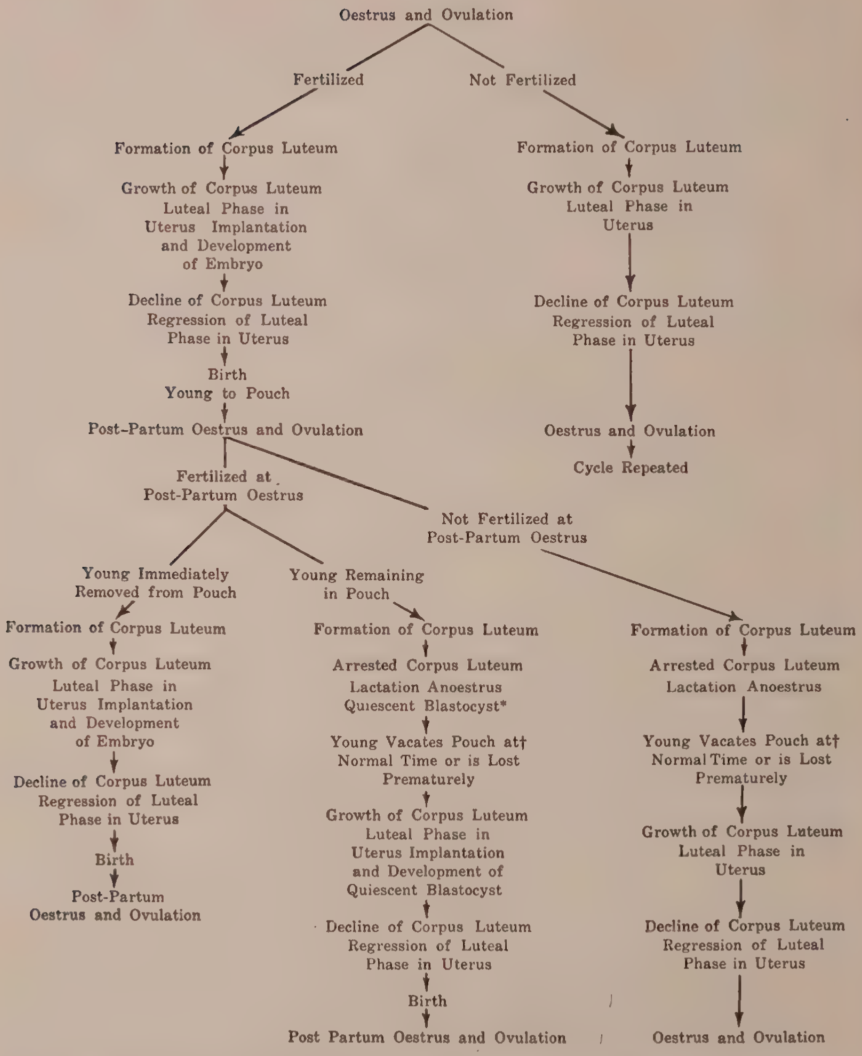
Delayed birth in marsupials has been recorded on several occasions prior to the publication of these results (e.g. Wood Jones 1924). Although delayed implantation is known in a number of eutherian species (e.g. Hamlett 1935; Brambell 1937; Hansson 1947) nobody appears to have considered this possibility in marsupials. Among eutherians only certain bats (Wimsatt 1942) are definitely known to retain live spermatozoa in the female tract for long periods. Many macropod marsupials exhibit at oestrus a swollen condition in the anterior vaginal canals (Wood Jones 1944; Pearson 1950) in which spermatozoa have been detected. It is considered (Pearson and de Bavay 1953) that these may serve to retain spermatozoa which then fertilize ova of two successive ovulations. As gestation and lactation anoestrus occupy about 6 months in macropods this calls for very prolonged storage. *Setonix* does not exhibit the swollen condition of the anterior vaginal canals at oestrus (Waring *et al.* 1955) displayed by other macropods. Having not yet conducted an experimental study on a macropod in which this condition occurs we cannot therefore entirely exclude the possibility of prolonged storage of spermatozoa, although we consider it unlikely. We can, however, definitely state that the possibility of sperm storage has been ruled out in *Setonix*. In this species delayed implantation, although of much greater duration, is strictly comparable with the observed phenomena in rats suckling large litters. Numerous publications on delayed implantation in eutherians have been made and the recent literature is reviewed by Hansson (1947). In addition to the species in which delayed implantation occurs during lactation other animals are known where environmental factors appear to be important in determining the delayed period (Hamlett 1935).

The mechanism of delayed implantation in eutherians has been the subject of wide controversy. Brambell (1937) stated that the decidual reaction could be evoked by irritation of the uterus during the free vesicle stage and considered that delayed implantation was not due to inactivation of the uterus. Krehbiel (1941), however, showed that more intense irritation is necessary to provoke deciduomata at the free vesicle stage than when implantation takes place. The precise hormonal interrelationships necessary to bring a uterus into a condition when it will form deciduomata on traumatization have not been fully elucidated. Oestrogen and progesterone together achieve this, but it is not clear which pituitary hormones bring about the secretion of oestrogen and progesterone in the intact animal. It is generally conceded that F.S.H. and L.H. achieve ovulation (and secretion of oestrogen) and formation of corpora lutea. There is some evidence, however, that a third agent, luteotrophin (either identical with prolactin or always a contaminant of it), is necessary to make the corpus luteum secrete progesterone and *inter alia* make the uterus sensitive to traumatization. Thus Sydnor (1945) found that if prolactin was injected into rats at oestrus, traumatization of the mucosa at dioestrus led to formation of deciduomata. This indicates that perhaps prolactin from the A.L.P. is the hormone responsible for the initiation of function of corpora lutea. Hansson (1947) showed that the corpora lutea were apparently inactive during the free vesicle stage in the mink. This author considered, however, that normal follicular development, ovulation, and corpus luteum formation indicated that the secretion of F.S.H. and L.H. was not disturbed, although the inactive corpora lutea indicated that the factor regulating progesterone secretion was not itself secreted. Hansson concluded this factor to be luteotrophin.

Attempts have been made by others to induce implantation and development in free unimplanted blastocysts by the use of oestrogen. In lactating rats implantation of the free blastocysts tends to take place at intervals corresponding to the time oestrus would normally be expected (i.e. 6-8, 10-11, 14-16, and 18-20 days after mating). Weichert (1942*b*) has recorded one case in which a lactating rat, inseminated at post-partum oestrus, had two sets of embryos differing in stage of development by 4½ days. Examination of the ovaries showed only one ovulation to have taken place. The same author (Weichert 1942*a*) attempted oestrogen replacement by giving small doses 4-14 days after parturition. He reported that implantation took place in 68 per cent. of cases.

The relationships of ovary and uterus during the phases of various reproductive processes in *Setonix* are shown diagrammatically in Figures 1 and 2. Our observations on this species show that during the period when the blastocysts are quiescent the corpus luteum does not develop. Until the removal of the young from the pouch lactation anoestrus occurs, during which the uterine glands are poorly developed and show no evidence of a luteal phase. Following removal of the pouch young, with associated growth of the corpus luteum, the uterus enters a luteal phase and the blastocyst begins normal development. We therefore think it most likely that lactation, together with nervous stimuli exerted by the foetus in the pouch, influences the ovary, by way of the A.L.P., so that the corpora lutea are kept in at least a partially inactive state. Until the luteal activity of the corpus luteum is resumed the conditions for embryonic development are unsatisfied.

Since our work has clearly shown that delayed birth in *Setonix* is due to the storage of an unimplanted blastocyst it is interesting to reassess earlier work on diprotodont marsupials with present knowledge in mind. Flynn (1930), while studying reproduction in *Bettongia cuniculus,* found he was unable to get the animals to breed in captivity. His material was therefore drawn from animals captured in the wild. Consequently most females studied were pregnant or carrying a foetus in the pouch and a blastocyst stage in one uterus. Although the pouch young were of different ages the blastocysts were all at approximately the same stages of development. These were most probably stored unimplanted blastocysts and their presence indicates that the same method of delayed birth as in *Setonix* may occur in the taxonomically widely separated *Bettongia*. In the absence


Oestrus and Ovulation
Fertilized
Not Fertilized
Formation of Corpus Luteum
Growth of Corpus Luteum Luteal Phase in Uterus Implantation and Development of Embryo
Decline of Corpus Luteum Regression of Luteal Phase in Uterus
Birth Young to Pouch
Post-Partum Oestrus and Ovulation
Formation of Corpus Luteum
Growth of Corpus Luteum Luteal Phase in Uterus
Decline of Corpus Luteum Regression of Luteal Phase in Uterus
Oestrus and Ovulation
Cycle Repeated
Fertilized at Post-Partum Oestrus
Not Fertilized at Post-Partum Oestrus
Young Immediately Removed from Pouch
Young Remaining in Pouch
Formation of Corpus Luteum
Growth of Corpus Luteum Luteal Phase in Uterus Implantation and Development of Embryo
Decline of Corpus Luteum Regression of Luteal Phase in Uterus
Birth
Post-Partum Oestrus and Ovulation
Formation of Corpus Luteum
Arrested Corpus Luteum Lactation Anoestrus Quiescent Blastocyst*
Young Vacates Pouch at† Normal Time or is Lost Prematurely
Growth of Corpus Luteum Luteal Phase in Uterus Implantation and Development of Quiescent Blastocyst
Decline of Corpus Luteum Regression of Luteal Phase in Uterus
Birth
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Growth of Corpus Luteum Luteal Phase in Uterus
Decline of Corpus Luteum Regression of Luteal Phase in Uterus
Oestrus and Ovulation

Fig. 2.—Diagrammatic representation of changes during the oestrous cycle, pregnancy, and lactation in *Setonix brachyurus*. The diagram begins at the top with a virgin or non-lactating female in oestrus. Compare with Figure 1, which gives the time relationships of the various reproductive phases.

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* Under conditions in the wild, on Rottnest I., the blastocyst apparently degenerates during seasonal anoestrus, which begins before the young vacates the pouch.

† Before the young vacates the pouch wild females, on Rottnest I., have entered seasonal anoestrus. These do not show growth of the corpus luteum and oestrus does not occur until the beginning of the following breeding season.

of controlled breeding experiments Flynn concluded that these blastocysts were stages in normal pregnancy. Flynn also observed oestrous symptoms in a female carrying a newly born pouch foetus, thus recording the occurrence of post-partum oestrus in this species. From these and other observations Flynn concluded that pregnancy and pouch life in *Bettongia* were of equal lengths, both occupying about 6 wk. Since we can, retrospectively, interpret Flynn's observations as meaning that in *Bettongia* there is delayed implantation as in *Setonix*, there is no longer any need to believe that the pouch life of *Bettongia* is only 6 wk. On the other hand we can be reasonably confident that no macropod marsupial has a pouch life as short as 6 wk.

This study has shown *Setonix* to be a well-adapted animal in its breeding behaviour. Periodic sexual receptivity of about 6 months (Sharman 1955) in the wild state allows a number of oestrous cycles to take place and thus gives the female the maximum number of opportunities to become pregnant. But the time of onset of anoestrus is such that no female may raise an offspring to the stage at which it leaves the pouch and then again give birth in the same year. This ensures that in the wild state (at least on Rottnest I.) most young enter the pouch at the same time of the year and that all have left the pouch at the beginning of the following breeding season. While the young are in the pouch a lactation anoestrus ensures that pregnancy cannot be carried through to its completion, thus preventing young of different ages occupying the pouch together. The significance of delayed implantation is, however, harder to assess. Two obvious advantages spring to mind: (*a*) That if animals only aggregate for short periods, as some macropods are reported to, the existence of a stored blastocyst offers obvious advantages if later appro- man 1955) in the wild state allows a number of oestrous cycles to take priate mating is prevented; (*b*) That if the pouch foetus is accidentally lost there is present, without further masculine intervention, a second young. We have some evidence, not quite conclusive, that a blastocyst cannot persist through seasonal anoestrus. In *Setonix* on Rottnest I. there is a seasonal anoestrus so the overt use of the mechanism is restricted to (*b*). We have incomplete evidence that some larger macropods also have a seasonal anoestrus and, like quokkas on Rottnest, the advantage would again be restricted to (*b*). On the other hand some macropods in the wild, like quokkas in captivity, are reported to exhibit no seasonal anoestrus. To these the full advantage of both (*a*) and (*b*) would accrue.

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THE AUSTRALIAN RHIPIDIINE PARASITES OF COCKROACHES (COLEOPTERA: RHIPIPHORIDAE)

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Summary

Eleven species of Rhipidiini, including *Nephrites nitidus* Schuckard, have been bred from Australian cockroaches. Twelve new species and four new genera are described and keys given for the identification of the five genera and 15 species known from Australia.

INTRODUCTION

Three species of Rhipidiini have been described from Australia but nothing has been recorded of their biology. The first, *Nephrites nitidus* Schuckard 1838, was described from Tasmania and was known only from the original description. Blackburn (1899) and Lea (1917) each described a species in the genus *Rhipidius*.

Recently, both sexes of *Nephrites nitidus* have been bred from *Platyzosteria* sp. (Blattinae) collected at Hobart, Tas., and triungulins have been hatched from field-collected egg-masses associated with empty female pupae. *Rhipidius australasiae* Blackburn has not been recognized. The holotype of *Rhipidius mollipes* Lea is in the South Australian Museum.

Recent studies of the group have shown that there are several genera and species represented in the Australian fauna. Eleven species, belonging to five genera, have been bred from cockroaches and the remaining two species collected under conditions similar to those occurring in the other species when these are collected in the field and not bred.

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BIOLOGY

The Rhipidiini are endoparasitic on cockroaches in those cases where the host is known. The fully mature larva emerges from the host dorsally at one of the posterior intersegmental membranes of the abdomen. This pupation of the parasite free of the host makes the recognition of the host difficult unless the parasites are bred from field-collected nymphal cockroaches.

The biology of the species differs somewhat between genera, but, in all, the mature larva leaves the host dorsally at an intersegmental membrane. The host continues to live for some considerable time after the emergence of the parasite (up to several days). The larva then finds a suitable situation, often portion of a bark-covered tree trunk, and pupates, shedding the larval skin. There seems to be some evidence that parasitized specimens of normally ground-dwelling species of cockroach migrate onto tree trunks when the larval parasite is fully matured. The effect may be similar to an oviposition urge. Pupae have only been found on eucalypts, generally smooth-barked, though possibly they occur on other trees and in other situations. The pupa is attached to either the living or the adhering dead bark of the tree by a few silken strands.

The female does not move far from the empty pupa on emerging. The male apparently seeks her there, for the eggs are laid in a mass around the empty pupa. In *Rhipidioides* the eggs lie in a single layer on the substratum, separate from each other and held in place by silken threads. In *Nephrites* the eggs form an irregular mass among silken threads.

Intact pupae of *Nephrites* were collected in early January at Hobart and all hatched within 10 days of collecting, the males taking somewhat longer than the females. At Canberra a second species has been reared and the two females took 4 and 6 days to emerge from the pupa. This was early in May. Adults of several species of *Rhipidioides* have been reared. At Canberra adults emerged in August, at Bendora in February, and at Tharwa in February. These localities are all close together within the A.C.T. but the species occurring at each locality is quite distinct. At Casterton and Orbost, Vic., adult females have been reared in April. The male of *Neonephrites* was bred at Tidbinbilla, A.C.T., in October, the female of *Paranephrites* from Lee's Spring, A.C.T., in March, and the female of *Neorhipidius* from Canberra in April.

Most of the adults have been collected in the late summer and autumn, from February to April, with only one species of *Rhipidioides* and one of *Neonephrites* in the spring, August and October respectively. An intense search for the species of *Rhipidioides,* which emerges in the spring at Canberra, would seem to indicate that that species is limited in its occurrence to that time of the year. In the autumn one finds a species of *Neorhipidius* occurring in the same host species.

There is a distinct correlation between host and some parasite genera. The species of *Nephrites* have only been bred from Blattinae (*Cutilia* and *Platyzosteria*), while species of *Rhipidioides* occur only in the two closely related subfamilies, Ectobiinae and Pseudomopinae. The other three genera are monotypic. *Neonephrites* and *Neorhipidius* occur in the Pseudomopinae and *Paranephrites* in the Panchlorinae. As mentioned above, a species of *Rhipidioides* and one of *Neorhipidius* occur in the same host species. The Pseudomopinae is the only subfamily from which more than one genus has been bred, and it includes three genera.

MORPHOLOGY

Beetles of this tribe are highly modified and show marked sexual dissimilarity in the adult stage. The adult males are winged but have the elytra strongly reduced and the hindwing somewhat expanded, while the adult females are wingless and larviform.

In many structures they resemble the Strepsiptera and can be differentiated from them only on a single main character. Strepsiptera lack trochanters, while they are distinct in the Rhipidiini. An apparent exception in the Rhipidiini is *Rhyzostylops* Silvestri 1905, which is not adult. It is the last larval instar of a form similar to, if not identical with, *Rhipidius*. When the last larval instar of the parasite leaves the host there is some delay before it settles down and pupates, casting the last larval skin in the process. There is another character on which the two groups had been separated previously. The tarsi of Strepsiptera are always isomerous and in Rhipidiini they have always been considered heteromerous. This is true with two exceptions. The female of all the species of *Rhipidioides* has all the tarsi four-segmented though the male shows the normal heteromerous condition of 5, 5, 4. The female of *Neorhipidius* also has all the tarsi four-segmented. The male of this genus is not known. There are other differences between the Rhipidiini and the Strepsiptera but they have only slight significance.

In the Rhipidiini the prothorax, though reduced, is not ring-like, the postscutellum is not well developed, the anal area of the wing is quite small, and radial venation occurs only in the more specialized genera. Strepsiptera form exarate pupae within the larval skin while the Rhipidiini form obtect pupae and shed the larval skin.

Rhipidiini and Strepsiptera possess similar endoparasitic habit, hypermetamorphosis, campodeiform first-stage larvae, berry-like eyes with distinct facets in both sexes, ramose male and simple female antennae, and diminution of the abdomen in the male.

The five genera of Rhipidiini recorded in this paper from Australia can be separated by the following keys.

KEYS TO AUSTRALIAN GENERA OF THE TRIBE RHIPIDIINI

Males

1. Maxillary palps wanting; antennae touching at the base; scutellum strongly narrowed anteriorly; hindwing without crossveins....*Rhipidioides*, gen. nov.
Maxillary palps present; antennae quite separate at the base; scutellum almost as wide anteriorly as posteriorly; at least 1 distinct crossvein in the hindwing 2

2. Tarsi short, apical segment of fore and middle tarsi longer than 1st segment, not quite as long in the hind tarsus; metasternum with posterior margin excised; elytra scarcely reaching the base of the abdomen.............. *Nephrites* Shuckard
Tarsi long, 1st segment the longest; metasternum without posterior margin excised; elytra extending some distance over the abdomen................ *Neonephrites*, gen. nov.

Females

1. Dorsal thorax not sclerotized; mouth-parts not distinguishable; antenna with only 2-4 distinct segments; (all tarsi 4-segmented)..*Rhipidioides*, gen. nov.
Dorsal thorax sclerotized; well-developed 3-segmented maxillary palps; antenna 11-segmented 2

2. Tarsi heteromerous (5, 5, 4)..3
All tarsi 4-segmented (head strongly dorsoventrally compressed; 1st segment of the maxillary palp widest towards the apex; antenna about 3 times the length of the palps; head strongly narrowed posteriorly)............. *Neorhipidius*, gen. nov.

3. Head not strongly dorsoventrally compressed, rectangular in lateral view; antennal segments 4-10 only slightly contracted at bases; apical segment of palp rounded at apex..............................*Nephrites* Shuckard
Head strongly dorsoventrally compressed, almost linear in lateral view; antennal segments 4-10 strongly contracted at bases; apical segment of palp ending in an acute spine.......................*Paranephrites*, gen. nov.

Genus RHIPIDIOIDES, gen. nov.

Genotype *Rhipidioides helenae*, sp. nov.

Male

Maxillary palpi wanting; antennae touching at their bases, their basal 3 segments short and stout, the apical 8 produced into long flabellae, head small and globular, the greater part of its surface being occupied by the strongly granulated eyes, which are only slightly excavate around the antennae and contiguous both above and below; elytra extremely short, scarcely reaching the base of the abdomen, very widely separated from each other, the interval between them at the base being about as wide as the head, scutellum strongly narrowed anteriorly; postscutellum only slightly developed, transverse; legs stout and hairy, the tibiae dilated towards the apex, which is devoid of spines, the tarsi heteromerous (5, 5, 4) and short, apical segment of tarsus subequal to the 1st except for the hind tarsus; hindwing without crossveins.

Female

Body soft, lacking continuous sclerotization except for the legs and their attachments and for portion of the head: surface of body covered with fine granules, each surmounted by a seta; head small, with very reduced eyes situated laterally behind the antennal insertion; mouth-parts not distinguishable; antenna with only 2-4 distinct segments, the 1 or 2 at base small, apical one enlarged, slightly expanded, with some indications of segmentation, more so in dorsal view: tarsi isomerous, all with 4 distinct segments and simple paired tarsal claws.

The female of this genus has a remarkable tarsal structure. The tarsi are all 4-segmented. The first representative of the Rhipidiini examined by the author was a female of this genus. It was only after considerable deliberation that it was rejected as a strepsipteron and considered in the Rhiphoridae. It differs fundamentally from the strepsipteron *Eoxenos* only in possessing small, though distinct, trochanters. There are also small differences in the mouth-parts and in the segmentation of the antenna.

KEY TO SPECIES* OF THE GENUS RHIPIDIOIDES

Males

1. Pronotum with a faint median longitudinal carina over its whole length (a distinct rounded carina on the pronotum above the insertion of the fore coxa; mouth style wider than long) .... *mollis*, sp. nov.
Pronotum with a faint median longitudinal carina over its anterior quarter (no distinct carina above the fore coxal insertion; mouth style distinctly wider than long) .... *nanus*, sp. nov.
Pronotum without median longitudinal carina 2

2. Pronotum with distinct anterolateral projection so that lateral margin is markedly concave (mouth style longer than wide) .... *helenae*, sp. nov.
Pronotum with only slight anterolateral projection, lateral margin slightly convex in middle, posterolateral projection strongly developed and sharply defined (mouth style slightly wider than long) .... *rubricatus*, sp. nov.

Females

1. Head with distinct posterolateral projection so that head appears triangular (antenna 2-segmented in both dorsal and ventral views) .. *adynatus*, sp. nov.
Head with posterolateral projection small, projecting only slightly more than eyes 2

2. Antenna only 2-segmented both dorsally and ventrally ...... *fuscatus*, sp. nov.
Antenna 2-segmented, but dorsally with indications of a 3rd segment .... *mollis*, sp. nov.
Antenna with more than 2 distinct segments 3

3. Antenna 3-segmented in both dorsal and ventral views ...... *ablepius*, sp. nov.
Antenna dorsally 4-segmented, less obviously so ventrally .... *helenae*, sp. nov.

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* The species *australasiae* Blackburn has been omitted as it has not been recognized.

RHIPIDIOIDES AUSTRALASIAE (Blackburn)

Rhipidius Australasiae Blackburn, 1899, Trans. Roy. Soc. S. Aust. 23: 59.

Blackburn gave a very short description of this species, quite adequate at the time for it was the first record of the genus in Australia.

Type.—**Holotype male in the British Museum.**

Type locality.—Eyre's Peninsula, S.A. (coll. Blackburn). The holotype was found crawling over some dead blowflies. The species has not been recognized.

RHIPIDIOIDES HELENAE, sp. nov.

Plate 1, Figs. 2, 6-8; Plate 2, Figs. 4-6; Plate 4, Fig. 6

Male

Length 5.5 mm; body black, elytra lighter discally, hindwings very deep fuscous, all legs with trochanter and femur pale (straw-coloured) and hind tarsus and fore coxa to some extent pale, bases of all tibiae somewhat pale, otherwise black; antenna over apical segment and bases and apices of flabellae pale; mouth style pale.

Pronotum setose, tapered anteriorly, anterolateral and posterolateral corners distinctly produced, front margin straight, posterior margin slightly produced, angled at meson, lateral margins distinctly concaved, pronotum without a median longitudinal carina, with only a faint raised area above fore coxal insertion; head small, subglobular, eye very large, extending anteriorly to the base of the antenna; mouth-parts reduced to a small style, slightly longer than wide; antennae contiguous at base, 1st segment short, much wider than long, 2nd and 3rd smaller, subequal, together about equal to the 1st, 3rd slightly produced laterally, 4th and succeeding segments strongly flabellate, 4th very short, succeeding lengthening slightly; elytra very reduced, extending slightly over the abdomen dorsally; mesonotum wide, wider than head, deeply, widely grooved at meson, posterior border slightly emarginate at meson; metathorax enlarged, scutellum narrowing rapidly almost to a point anteriorly and reaching the anterior margin of the segment, scutum large, extending laterally almost to the posterior border of the scutellum, postscutellum transverse, developed only at the meson, half as wide as the scutellum; 1st abdominal segment large, half as long as scutellum, tapering slightly, apex rounded-truncate; fore and middle tarsi short, segments decreasing regularly in length and thickness except that the 5th is subequal in length to the 1st, hind tarsus about as long as fore tarsus, 1st segment longer than 4th, which is subequal to 2nd and 3rd combined; metasternum with a median longitudinal groove posteriorly; hind coxa laterad divided longitudinally by an unsclerotized area.

Hindwing 3 times as long as elytra; venation reduced and crossveins absent; costal margin with a short basal thickening ending just beyond a slight indentation; no distinct *Sc* and R_1 but strong folds marking the position of these veins, particularly the convex R_1; then follows a distinct narrow vein, raised on a convex fold, well spaced from R_1 and extending more than half way to the wing margin; then follow another 2 veins with the same basal attachment lying close together but well separated from the vein above, the 1st is a strong vein lying in a concave fold except at base and the succeeeding one is weak and reaches only half way to the wing margin. These 3 veins are considered to be *M*, *CuA*, and reduced *CuP*. Then follow the anal veins, which are widely separated from *Cu*; 1*A* reaches the wing margin; 2*A*, lying close to it, is very short and there appears to be a short jugal. The wing is very similar to that of Strepsiptera but is not as expanded and lacks the detached veins at the apex of the wing.

Female

Length preserved 10.0 mm, with the antenna about 1.0 mm; body darkish at extremities and laterally, lighter above, except narrowly at meson, particularly on thorax, ventrally pale at meson.

Thoracic segments of subequal length, 1st a little shorter, abdomen tapering after the 3rd segment to the pointed apex, 8th and succeeding segments very small; sclerotized attachments for the legs, dorsally, distinctly raised above the body surface, particularly on prothorax, anterior margins almost straight, strongly raised and heavily sclerotized over the posterior margin; tarsi very short, segments decreasing slightly except that the apical is the longest, segmentation markedly oblique over the basal segments in lateral view; head produced beyond the antennal insertions, rather triangular in dorsal view but no marked posterolateral projection; eye situated well behind the insertion of the antenna, almost circular in outline, but a little produced dorsoventrally; antenna in dorsal view appearing 4-segmented, but the suture between the 3rd and 4th segments not very clear, ventrally with only 3 distinct segments, the 2 basal ones and the enlarged apical one, in dorsal view basal segment almost square, with convex distal margin, 2nd smaller than 1st, slightly over half the width of the first, strongly convexed distal margin, 3rd with sutures very oblique, extending proximally to touch the 1st segment laterally, distal margin not as convex as proximal, and this suture indistinct, remainder of antenna formed of an enlarged, distally expanded segment, ventrally the suture between the 3rd and apical segments is not complete and the 2nd segment is wider than the 1st; ventral area between the insertion of the antenna and eye polished but with limited longitudinal striae, not heavily sclerotized; mouth-tube not markedly truncate in lateral view, anterior margin strongly convex in dorsal view, dark-coloured; ventrally the head is not heavily sclerotized, darkened only at mouth-tube and at meson behind this and at antennal insertions.

Types.—Holotype ♂, allotype ♀, and triungulins in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Canberra, A.C.T., holotype (18.viii.1950, H. M. Cane), allotype (17.viii.1950, H. M. Cane).

Host.—Bred from the cockroach *Escala longiuscula* (Walker) or *Escala cucumducta* (Walker) (subfamily Pseudomopinae).

Only the type specimens are known.

RHIPIDIOIDES RUBRICATUS, sp. nov.

Plate 1, Fig. 1; Plate 4, Fig. 5

Male

All legs with trochanter, femur, extreme base of tibia, and apex of tarsus, pale (straw-coloured), fore and middle coxae also pale; antenna, except apical segment, all dark; mouth style pale.

Mouth-parts reduced to a small, slightly wider than long, style; pronotum with lateral margin slightly convex in middle, anterolateral projection small, posterolateral projection large, sharply defined, pronotum without a median longitudinal carina, without a distinct carina above the fore coxal insertion.

Types.—Holotype ♂ and paratype ♂ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Bendora, A.C.T. (6.ii.1951 and 6.xii.1950, H. M. Cane).

Host.—Bred from the cockroach *Choristima* sp. (subfamily Ectobiinae).

Specimens examined.—Also two males bred from *Choristimodes* sp. 26.xi.1951, collected at Blundells, A.C.T. (2.xi.1951, H. M. Cane).

Very similar to *helenae* but differing in colouring and in the shape of the pronotum and the mouth-parts.

RHIPIDIOIDES NANUS, sp. nov.

Male

Length 4.0 mm; body black, joints of thorax lighter, elytra lighter discally, hindwings deep fuscous, all legs with trochanter and femur pale (straw-coloured) and fore and middle coxae pale, all tarsi dark, tibiae dark except at base, antenna all dark, mouth style dark.

Pronotum setose, anterolateral corners rounded and lateral margins almost straight except at posterolateral projection, pronotum with a faint median longitudinal carina over its anterior quarter, without a distinct carina above the fore coxal insertion; head small, subglobular, eye very large, extending anteriorly to the base of the antenna, mouth-parts extremely reduced, an almost imperceptible, wider than long, style; antenna with 3rd segment slightly produced laterally, succeeding 8 segments laterally uniflabellate; elytra reduced, extending slightly beyond the thorax, dorsally metathorax enlarged; mesonotum wide, wider than head, deeply widely grooved at meson, posterior border distinctly emarginate at meson; scutellum narrowing rapidly almost to a point anteriorly, scutum large, extending almost to the posterior border of the scutellum; postscutellum transverse, half as wide as scutellum, a short groove at meson; 1st abdominal segment large, half as long as scutellum, tapering posteriorly but with transverse apex; all tarsi short, segments decreasing regularly in size and thickness except that apical is subequal in length to 1st, though less so in the hind tarsus; metasternum with a median longitudinal groove posteriorly; hind coxa laterally divided longitudinally by an unsclerotized area.

Type.—Holotype ♂ and paratype ♂ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Ten miles SW. of Ayr, Qld. (6.viii.1950, E. F. Riek) taken under bark of eucalypt.

This species differs from *helenae* in the pale fore and middle coxae, dark hind tarsus, dark antenna as well as the more reduced mouth-parts, and different pronotum. Only the two males are known.

RHIPIDIOIDES MOLLIS, sp. nov.

Male

All legs with trochanter and femur reddish yellow, fore and middle coxae also reddish yellow, hind coxa darkened; tibiae, except at base, and tarsi black; antenna all dark; mouth style dark.

Mouth-parts reduced to a small, wider than long, style with pointed apex; pronotum with a faint median longitudinal carina over its whole length, pronotum with the lateral margin slightly concave, widening markedly caudally to the posterolateral projection, pronotum with a distinct rounded carina above the fore coxal insertion merging with the posterolateral projection caudally.

Female

Length preserved 6.5 mm, excluding the antennae of about 1.0 mm; body almost uniformly dark, but with a distinct, light, median, ventral, longitudinal band extending from the thorax almost to the apex of the abdomen; head and apex of abdomen mostly very dark.

Sclerotized attachments for the legs, all dorsally raised above the body surface, possibly more so on the prothorax, anterior margins straight or almost so, posterior margin not strongly raised; tarsi very short, 1st and 2nd segments subequal, shorter than the 3rd, 4th subequal to 3rd or very slightly longer, segmentation of the tarsi almost transverse, not markedly oblique in lateral view; head squarish, directed rather ventrally, with a slight forward projection between the antennae; eye situated some distance behind the antennal insertion, strongly produced dorsoventrally, more than twice as long as wide, posterior border not distinctly raised;

no obvious posterolateral projection of the head; antenna, in ventral view, appearing only 2-segmented, but in dorsal view there is an additional faint convexed suturing of the apical segment near its base, basal segment considerably longer than wide, distal margin strongly convexed, apical segment expanded, flattened, slightly expanded at the rounded apex, with an obvious constriction on the mesal side towards its base, at the level of the indistinct dorsal suture; ventral area between insertion of antenna and eye glabrous; mouth-tube short, obliquely truncate in lateral view, anterior margin convex in dorsal view; ventrally head heavily sclerotized only at meson behind the mouth-tube and for a small oblique line lying close behind the eye and directed anteromesally.

Types.—Holotype ♀, allotype ♂, and 2 paratype ♀♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Holotype from Tharwa, A.C.T. (14.ii.1951, H. M. Cane), allotype from Canberra, A.C.T. (11.v.1951, E. F. Riek).

Host.—Holotype bred from cockroach, *Escala longiuscula* (Walker) or *E. cucumducta* (Walker) (subfamily Pseudomopinae). Allotype and two paratypes found dead together under bark.

The female of this species is distinctive both in colour and structure, particularly of the antenna. The male has a distinctive pronotum with a faint median longitudinal carina. The two females found dead are rather shrivelled but the antennal and tarsal structures are clear.

RHIPIDIOIDES ABLEPTUS, sp. nov.

Female

Length preserved 10.0 mm, with the antenna about 1.0 mm; body darkish at extremities and laterally, lighter above, except narrowly at meson, particularly on thorax; ventrally very pale at meson and pale area bordered with a narrow dark line.

Thoracic segments enlarging somewhat posteriorly; abdomen tapering, particularly after the 6th segment, 8th and succeeding segments very small; sclerotized attachments for the legs raised slightly above the body surface, not markedly so on the prothorax, anterior margins almost straight, posterior slightly raised; tarsi very short, 2nd segment from above equal to or slightly exceeding in length the 1st, 3rd shortest, 4th as long as 2nd, segmentation markedly oblique in lateral view particularly over basal segments; head produced beyond the antennal insertions, rather triangular in dorsal view but with only a slight, though obvious, rounded, posterolateral projection from the head; eye situated some distance behind the insertion of the antenna, oval in shape, twice as long as wide, with its posterior border distinctly raised; antenna 3-segmented in both dorsal and ventral view, dorsally 1st segment about as long as wide, distal border strongly convex, second much wider than long, as wide as 1st, 3rd or apical segment very large, slightly contracted at base and expanded irregularly at apex, twice as long as the 1st 2 segments; segments of the antenna triangular in cross section, apical segment less regularly so in middle; ventral area between insertion of antenna and eye glabrous; mouth-tube obliquely truncate in lateral view, anterior margin evenly rounded in dorsal view, paler in colour than rest of anterior half of head; ventrally head heavily sclerotized to a transverse line slightly behind the level of the eye.

Type.—Holotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Fifteen miles NW. of Casterton, Vic. (14.iv.1951, H. M. Cane).

Host.—Bred from cockroach *Balta patula* (Walker) (subfamily Ectobiinae).

The larval parasite emerged from the host on April 27 and the adult parasite emerged on April 30, possibly, though not likely, on the day before, so that the pupal stage lasted only 3 days. Only the holotype is known.

RHIPIDIOIDES ADYNATUS, sp. nov.

Female

Length preserved 10.0 mm; colouring and shape as in other species.

Sclerotized attachments for the legs raised slightly above the body surface, particularly so on the prothorax, anterior margins strongly excavated in the middle, posterior margin, particularly of meso- and metathorax strongly raised; tarsi very short, dorsally the 1st 2 segments subequal, 3rd and 4th a little longer, 4th slightly the longer, segmentation markedly oblique in lateral view, particularly over basal segments; head distinctly triangular in dorsal view, a distinct, acute, posterolateral projection from the head, giving the pronounced triangular shape to the head; eye very small, elongate, only slightly raised; antenna only 2-segmented in both dorsal and ventral view, but ventrally with some indication of a 3rd segment, basal portion of antenna distinctly triangular, dorsally 1st segment about twice as long as wide at base, tapering to strongly convex apex, with a slight projection on the mesal margin at about the middle of its length, 2nd or apical segment expanding slightly, but then showing a very marked constriction on its mesal margin before expanding rapidly to the very broad apex; ventrally the 1st segment is almost truncate at apex; apical segment distinctly triangular in section; ventral area between the insertion of the antenna and the eye not entirely glabrous but with a few low rugae and tubercles. This rather smooth area is sharply marked off from the raised mesal zone, which is coarsely punctate. Mouth-tube very short, truncated, somewhat heart-shaped in frontal view, almost flush with the head, and protruding only slightly; ventrally head heavily sclerotized to a transverse line lying quite behind the eyes and produced backwards to an obtuse point towards the lateral margin.

Type.—Holotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Eighteen miles NE. of Orbost, Vic. (21.iv.1951, H. M. Cane).

Host.—Bred from a species either of *Escala* or an undescribed genus of Pseudomopinae.

The larval parasite emerged from the host on April 30 (or possibly 29) and the adult parasite emerged on May 2. Pupation occurred at least after April 27 so that the pupal stage lasted not more than 5 and most probably only 3 days. Only the holotype is known.

RHIPIDIOIDES FUSCATUS, sp. nov.

Female

Length preserved 9.5 mm, excluding the antennae of about 1.0 mm; body uniformly dark except ventrally, at meson widely, at the intersegmental areas of the abdomen; head very dark.

Sclerotized attachments for the legs dorsally not raised very much, anterior margins rather curved, posterior margins raised; tarsi short, 1st segment the shortest, 2nd and 3rd subequal, 4th longest, about twice as long as 1st, segmentation of tarsi very oblique in lateral view; head squarish, directed rather ventrally, with a median projection between the antennae; eye situated some distance behind the antennal insertion, small, strongly produced dorsoventrally, more than twice as long as wide; no obvious posterolateral projection of the head; antenna in both dorsal and ventral view only 2-segmented, in ventral view basal segment very obliquely truncate at apex, only about one-third the size of the apical segment, apical segment rounded at apex, swollen over apical half so that the cross section is circular, dorsally the basal segment is wider than long, transverse at apex, apical segment rounded at apex, anterior border slightly convex, posterior border very slightly concave at middle of its length; ventral area between insertion of antenna and eye strongly ornamented; mouth-tube rather long, apex with 2 small, distinct lobes, rounded; whole of head heavily sclerotized and ornamented.

Type.—Holotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Twelve miles W. of Moree, N.S.W. (19.viii.1951, A. Dyce), parasite emerged from host 7.iv.1952.

Host.—*Ellipsidion affine* Hebard (subfamily Pseudomopinae).

The female has a most distinctive antenna and heavily ornamented head. Only the holotype is known.

Genus NEPHRITES Shuckard

Nephrites Shuckard, 1838, Ent. Mag. 5: 512.

Genotype *Nephrites nitidus* Shuckard, 1838, op. cit. 513 (original designation).

Male

Elytra short and broad, scarcely reaching the base of the abdomen above, widely separated at base, the interval between about as wide as the head; distinct, 2-segmented maxillary palpi arising from a fused base; head small, rectangular from above, with sharply truncate and carinate posterior border; eyes large and bulbous, but occupying only the anterior portion of the head, particularly ventrally, contiguous both dorsally and ventrally, facets largest mid-laterally; antennae distinctly separated at bases, 1st segment cup-shaped, somewhat longer than wide, 2nd and 3rd short, together subequal to the 1st, 3rd slightly produced laterally, succeeding 8 segments strongly, closely uniflabellate; legs stout and hairy, the tibiae clubbed at apex, which is devoid of spines, the tarsi heteromerous and short, tarsal claws serrate, 5th segment of the fore and middle tarsi longer than the 1st, 4th of hind tarsus not quite as long as 1st; posterior margin of the pronotum slightly produced at meson; scutellum only slightly narrowed anteriorly; postscutellum poorly developed, forming a narrow transverse band, sclerotized to the lateral margins; metasternum without a median longitudinal groove but posterior margin excised; hindwing with *Sc* and *R* fused to the costa close to the base to form a much thickened area, with a long crossvein between the thickened *Sc-R* and *Cu* at the apical third, a detached vein between *Cu* and *1A*.

Female

Body with head and portion of thorax sclerotized; antennae widely separated at base, 11-segmented, with only the apical segment slightly produced, segments 4-10 disk-shaped, with contracted base, much wider than long; head not strongly dorsoventrally compressed, in lateral view almost as deep as long; mouth-parts reduced, but maxillary palpi very large, elliptical in cross section, inflated, particularly the basal segment, 2nd more rounded, 3rd minute, rounded, 1st segment widest at middle but almost as wide at base; eye reduced, lying behind the antennal insertion, not half as wide as long, with at least 1 enlarged facet at the middle of its posterior border; tibiae without apical spurs, outer margin smooth but setose; fore and middle tarsi 5-segmented, hind tarsus 4-segmented, apical tarsal segment longest in all tarsi, others decreasing regularly from 1st.

The male of *Nephrites* differs markedly from *Rhipidioides*, particularly in the structure of the mouth-parts, wing venation, in the shape of the head and the thoracic sclerites, such as scutellum and postscutellum, and in the hind coxa. The female differs noticeably in the structure of the mouth-parts and antennae.

NEPHRITES NITIDUS Shuckard

Plate 1, Figs. 3 and 4; Plate 3; Plate 4, Figs. 2-4

Nephrites nitidus Shuckard, 1838, Ent. Mag. 5: 513.

Male

Length 5.0 mm but in life about 7.0 mm, with abdomen extending some distance beyond the apex of the hindwings; body black, elytra lighter at apex, hindwing deep fuscous with blackish veins; legs all black with tarsi lighter ventrally; antenna black, lighter over apices of flabellae and apical flabellum.

Pronotum setose, strongly tapering anteriorly, anterior corner rounded, posterior corner produced, acute, lateral margin slightly produced at middle, gently concaved behind, an irregular pitting of the dorsal surface anterolaterally; head small, rectangular, somewhat expanded and carinate at posterior margin; eye large but occupying only the anterior portion of the head, particularly ventrally, contiguous both dorsally and ventrally, facets largest mid-laterally; maxillary palpi distinct, arising from a fused, wider than long, base; antennae well separated at the base, 1st segment cup-shaped, not quite as long as wide, 2nd small, transverse, 3rd somewhat larger, slightly produced laterally, succeeeding segments short, strongly uniflabellate; elytra short and rather broad, just extending onto the abdomen dorsally; mesonotum wide, much wider than head, deeply grooved anteriorly at meson, subacutely rounded posteriorly at meson; metathorax enlarged, scutellum narrowing only very slightly anteriorly, slightly convexed in the middle, reaching the anterior border of the segment, scutum limited to the lateral third, extending almost to the posterior border of the scutellum; postscutellum transverse, posterior border almost straight, sclerotized to the lateral margin, wider than scutellum; abdominal segments large, decreasing gradually posteriorly, 1st segment half as long as the metathorax and as wide, heavily sclerotized; tarsi short and rather stout, segments decreasing regularly in size except that the apical is longer than the 1st, except in the hind tarsus where it is slightly less than the 1st; metasternum without a groove at the meson but with the posterior margin excised at the meson; hind coxa laterally not subdivided, entirely sclerotized.

Hindwing 3 times as long as the elytra; venation reduced but 2 crossveins present; *Sc* and *R* fusing with the costa at a level of the apex of the elytra to form a strong, much thickened vein, *Cu* a strong vein dividing the wing into 2 almost equal areas, a long crossvein from *Cu* to the fused *C-R* at the apical third and at this point *Cu* curving down strongly to the wing margin, below *Cu* a detached vein extending from the wing margin towards the base, 1*A* a strong vein with a slight curving near the margin, 2*A* weaker, with a crossvein to 1*A* from about its middle, a strong transverse jugal at the base of the wing.

Female

Preserved length 8.5-11.0 mm; colour of sclerotized portions black, abdomen with a mottled grey appearance.

Head very small and flattened on the dorsal surface, almost half the width of the pronotum, as deep as long in lateral view; eye very small, dorsoventrally elongated, a little longer than the antennal insertion, not half as wide as long, with an enlarged facet at the middle of the posterior margin; a small truncate frontal projection between the antennae; antennae inserted widely apart, directed laterally, 11-segmented, 1st segment much the largest, about twice as long as wide at base, apex half as wide again as base, second segment disk-shaped but almost quadrate, 3rd with a distinctly contracted base, 4th somewhat longer than 3rd, distinctly longer than the succeeding segments, apical segments very slightly expanded laterally; maxillary palpi greatly expanded, bulbose, together almost as wide as the head, in lateral view longer than the head, 1st segment much the largest, somewhat wider in middle than at base, 2nd segment only about half the size of the 1st, its base as wide as the apex of the 1st, 3rd rounded at apex, also expanded at base, minute; pronotum strongly arched, expanding rapidly posteriorly, posterior margin almost straight, lateral margin rounded, projecting lateral portion distinct, meso- and metanota of increasing size, with both anterior margins almost straight, posterior convex, lateral projections decreasing in size; surface of all nota reticulate and setose; abdominal segments decreasing regularly in size, 8th and succeeding partially hidden; prosternum sclerotized in part across the meson, mesosternum with a narrower, almost linear, sclerotized area, metasternum not sclerotized; legs short, trochanters subequal, femora expanded in middle, tibiae clubbed at apices, tarsi short, segments decreasing regularly in size except that the apical is much the longest; tarsal claws simple, slightly flattened at base.

Type.—Location not known.

Type locality.—Tasmania.

Distribution.—TASMANIA: Hobart (Jan. 1951, E. F. Riek), 2 ♂♂, 3 ♀♀, collected as pupae under bark of eucalypt; Hobart (4.i.1953, E. F. Riek), 2 ♀♀.

Host.—Bred from *Platyzosteria* sp. (Blattinae) in January 1953.

Pupae of this species were collected in the field from under the rough bark, mostly at the base of otherwise smooth-barked eucalypts. The old bark persists at the base for several seasons and empty pupae at various stages of decomposition were quite numerous. Only four intact pupae (and one dead female) were obtained, though there were a small number of empty female pupae of this season surrounded by their egg-masses. The eggs were only freshly laid, there being little embryonic development. Two intact pupae were found side by side as though they had emerged from the one host. One was a male and the other a female, but the female was of abnormally small size, being very little larger than the male pupa. The female emerged 4 days before the male. Emergence always took place very early in the morning. In the males the wings were pale and the abdomen still distended at 7.0 a.m. By 9.0 a.m. the colour was fully developed and the specimens very active, walking round rapidly in the pill-box. The apex of the abdomen, which extended somewhat beyond the apices of the hindwings, was directed vertically upwards and showed constant agitation as the specimens walked about.

On the other hand the female was never very active and moved only very slowly when at all. One female remained alive in a pill-box for several days and although not mated, laid a number of eggs before dying, without moving from the egg-laying position. These eggs did not hatch.

Male pupae take at least 10 days and female 6 days to hatch but the upper limit is not known.

NEPHRITES AUSTRALIS, sp. nov.

Plate 2, Figs. 1 and 2

Female

Length preserved 10-12 mm; colour of sclerotized portions black, antenna reddish, tibiae and tarsi light, abdomen with very pale mottled greyish appearance.

Head very small, somewhat flattened above, but still slightly convex, in lateral view almost as deep as long; eye very small, dorsoventrally elongated, longer than the antennal insertion, not half as wide as long, with at least 1 enlarged facet at the middle of the posterior margin; a small projection, with rounded apex, and with a median longitudinal carina, in front of the antennae; antennae inserted widely apart, directed laterally, 11-segmented, 1st segment much the largest, about twice as long as wide at base, apex expanded, half as wide again as base, 2nd disk-shaped, much wider than long, succeeding segments with constricted bases, particularly 3rd, all much wider than long except the 4th, which is noticeably longer than the others, apical segment very slightly expanded laterally; maxillary palpi greatly expanded, bulbous, together almost as wide as the head, in lateral view much longer than the head, 1st segment much the largest, slightly wider in the middle than at base, 2nd only about half the 1st both in length and width, expanded in the middle, contracted at base, 3rd rounded with the apex slightly produced, base very constricted, minute; head and dorsal thorax densely setose, but setae short; pronotum strongly arched, expanding rapidly posteriorly, posterior margin almost transverse, lateral margin rounded, slightly emarginate behind, projecting lateral portion distinct; meso- and metanota of increasing width, anterior margins almost transverse, posterior convex; lateral projection of mesonotum distinct, narrow, that of metanotum indistinct; surface of all nota reticulate and setose; abdominal segments decreasing regularly in size, 8th and succeeding partially hidden, ovipositor longer than wide; prosternum sclerotized in part across the meson, mesosternum with a much wider sclerotized area, its anterior section irregularly darkened and with a slight median ventral projection less sclerotized than the surrounding area, metasternum not sclerotized; legs short, trochanters subequal, femora expanded in the middle, tibiae clubbed at the apices, tarsi short, segments decreasing regularly in size except that the apical is much the longest, basal segments somewhat produced laterally on the anterior surface, tarsal claws simple, hooked, expanded at base.

Types.—Holotype ♀ and paratype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Doughboy, N.S.W. (8.v.1951, B. Wetherley).

Host.—Reared from the cockroach *Cutilia* sp. (subfamily Blattinae) collected 23.i.1951. Both females emerged from the one host.

This species differs from the Tasmanian *nitidus* in the structure of the antenna, particularly of the second segment, in the more rounded palps with small, almost globular apical segment, and in the differently sclerotized mesosternum. The head shape and the frontal projection also differ.

NEPHRITES MAXIMUS, sp. nov.

Female

Length preserved 14 mm, with a maximum width of over 5 mm; colour of sclerotized portions deep black, palps shining jet-black, antennae and antennal insertions reddish, tibiae and tarsi light, abdomen with mottled greyish appearance.

Head very small, flattened above; eye very small, dorsoventrally elongated, kidney-shaped, about as long as the antennal insertion, without obviously enlarged facets; antennae inserted widely apart, directed laterally, 11-segmented, 1st segment much the largest, more than twice as long as wide at base, apex quite expanded, almost twice as wide as base, produced on lower side to a pointed apex, 2nd segment quadrate or slightly longer than wide, succeeding segments with constricted bases, particularly 3rd, all much wider than long except the 4th, which is noticeably longer than the others, apical segment bulbous, slightly expanded laterally; maxillary palpi greatly expanded, bulbous, very similar to those in *australis;* head and dorsal thorax densely setose but setae short; pronotum strongly arched, expanding rapidly posteriorly, surface of all nota reticulate as well as setose; attachments of legs obscured; segmentation of legs as in *australis.*

Type.—Holotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Blundells, A.C.T. (26.i.1954, H. M. Cane).

Host.—Not known. The dead pupa, from which the adult was extracted, was collected under the loose bark of a eucalypt.

Only the holotype is known. The species appears to be more closely allied to *australis* than to *nitidus,* having the same type of palps as in *australis.* However, the antenna is distinctive, particularly the basal segment. The species is of large size.

NEPHRITES sp.

Plate 4, Fig. 1

A species of this genus occurs in the cockroach *Platyzosteria castanea* (Brunn.) (subfamily Blattinae) but only an imperfect female has been reared at Canberra (15.ii.1951, E. F. Riek). This specimen was collected soon after the mature larval parasite had left the host. It was still almost white in colour and had only commenced to cast the larval skin and pupate. In leg structure it was rather similar to *Rhyzostylops* Silverstri, having no trochanter and unisegmented tarsi. Unfortunately the pupa formed was imperfect and the adult had to be dissected from the pupa. The specimen is of much the same size as the holotype of *maximus*.

Genus PARANEPHRITES, gen. nov.

Genotype *Paranephrites xenus*, sp. nov.

Female

Body with head and portion of thorax sclerotized; antennae short, only about twice the length of the palps, widely separated at the base, 11-segmented, with only the apical segment very slightly produced, segments 4-10 cup-shaped, with strongly narrowed bases and slightly expanded laterally; head strongly dorsoventrally compressed, upper surface flat, posterolateral margins carinate; mouth-parts reduced but maxillary palpi very large and flattened, particularly the basal segment, less so the 2nd, 3rd quite small and with a sharp spine at apex, 1st segment widest at middle but greatly expanded at base; eyes very reduced, lying behind the antennal insertion and somewhat longer than it, not half as wide as long, with an enlarged facet at the middle of its posterior border; frontal projection between the antennae truncate; tibiae without apical spurs, upper surface slightly crenulated, tarsi heteromerous (5, 5, 4), apical tarsal segment longest in all tarsi, 1st segment longer than wide in hind tarsus, less in fore and middle tarsi; setae of head and thorax not conspicuous and surface smooth or only very slightly crenulated.

This genus, which is known only from the female, may be based on an aberrant species of *Nephrites*. However, the antenna and palp have a quite distinct structure and the head is shaped differently than in the species of *Nephrites* described above.

PARANEPHRITES XENUS, sp. nov.

Female

Length 13 mm. Colour in spirit brownish black with black head and thorax which occupy little more than a quarter of the total length.

Head very small and strongly flattened dorsally, only a third the width of the pronotum; eyes small, occupying the anterolateral area just behind the antennal insertion but longer than it; head with a small truncate projection in front of the antennae; antennae inserted widely apart, directed laterally, 11-segmented, 1st segment largest, twice as long as wide, succeeding segments moniliform with markedly contracted bases, apical segment somewhat expanded laterally; maxillary palpi greatly expanded, together almost as wide as the head, in lateral view longer than the head, 1st segment much the largest, 2nd only half both as long and as wide as 1st, 3rd quite small, pointed at apex; pronotum strongly arched, deeply excavated in front and strongly convex behind, lateral margin rounded, projecting lateral portion distinct; meso- and metanota of increasing size, with straightening of both anterior and posterior margins and with less lateral projection; surface of all nota polished, with shallow irregular punctures; abdominal segments decreasing in size after the 2nd, 8th and succeeeding segments partly hidden; prosternum sclerotized in part across the meson, mesosternum with a narrower, almost linear, sclerotized area, metasternum not sclerotized; legs short and stout, middle and hind trochanters subequal, somewhat larger than fore trochanter, femora expanded, tibiae clubbed at apices, tarsi short, segments decreasing regularly in size except that the apical is much the longest; tarsal claws simple, slightly flattened at base.

Type.—Holotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Lee's Spring, A.C.T. (22.iii.1938, M. F. Day).

Host.—Bred from cockroach *Oniscosoma granicollis* (subfamily Panchlorinae).

Only the holotype is known.

Genus NEONEPHRITES, gen. nov.

Genotype *Neonephrites partiniger*, sp. nov.

Male

Elytra short, but extending some distance beyond the base of the abdomen, separated at the base, but the interval between them only about half the width of the head; distinct 3-segmented maxillary palpi present; head small, squarish from above, eyes very large, deeply excavate in front around the base of the antenna, contiguous over a short distance above and widely so below, laterally extending close to the posterior border; antennae distinctly separated at their bases, 1st segment considerably longer than wide, longer than 2nd and 3rd combined, succeeding 8 segments strongly, closely uniflabellate; legs stout and hairy, the tibiae devoid of apical spines, the tarsi heteromerous and rather long, 1st segment of tarsus considerably longer than any other segment, hind tarsus with 3rd segment shortest, 4th subequal to or longer than 2nd; posterior margin of the pronotum almost straight, at least not produced at meson; scutellum only slightly narrowed anteriorly; postscutellum very small, transverse, almost completely hidden by a small posterior projection of the scutellum;

metasternum without a longitudinal groove or excised margin; venation as in *Nephrites* but 2*A* and the crossvein to 1*A* not distinct and the crossvein in the apical region of the wing incomplete.

Although the genus resembles *Nephrites* in many characters the differences are too marked for it to be considered congeneric. There are the less reduced elytra, quite different head shape with different eye and antenna structure, different scutellum and metasternum, and hind coxae and longer tarsi with different proportions to the segments.

Rhipidius mollipes Lea is considered to belong to this genus. The proportions of the hind tarsal segments differ from those of the genotype but in other characters they are closely similar. The two species can be separated readily on colour as well as on structural characters.

NEONEPHRITES PARTINIGER, sp. nov.

Plate 1, Fig. 5

Male

Length 6.5 mm; body black, marked with reddish yellow, black except for prothorax and mesothorax; head, elytra, metathorax, and abdomen black; all legs with coxa, trochanter, femur, and basal portion of tibia reddish yellow, remainder of leg dark; antenna black, with 2nd and 3rd segments and basal portion of all flabellae light.

Pronotum setose and punctate, tapering anteriorly, anterolateral corners rounded, posterolateral corners produced, acute, otherwise lateral margin more or less straight or slightly convex, upper surface without grooves, posterior margin almost straight, slightly emarginate at meson; head small, almost square from above; eye large, anteriorly strongly emarginate around the antenna, contiguous above on its posterolateral border, with 3 distinct, small, blunt spines, the upper one the largest; mouth-parts very reduced but stout, 3-segmented maxillary palpi present, palps somewhat longer than the 1st segment of the antenna; antennae quite separate at base, 1st segment stout, considerably longer than wide, 2nd and 3rd wide, subequal, together less than the 1st, 3rd not produced, succeeding 8 segments strongly uniflabellate, the segments very short but increasing slightly apically; elytra reduced, but extending over the basal portion of the abdomen to the 3rd segment; mesonotum wider than head, a wide open groove at meson anteriorly, disappearing posteriorly, hind margin straight or very slightly rounded at meson; metathorax enlarged, scutellum with almost parallel sides but narrowing slightly over the anterior half, posteriorly rounded, somewhat produced and obscuring the linear postscutellum; 1st abdominal segment large, two-thirds the metathorax; tarsi rather long, all with segments decreasing regularly in length except that the apical is subequal to the 2nd, 1st segment of hind tarsus relatively long; metasternum without a median longitudinal groove posteriorly and posterior margin not excised; hind coxae only partially fused to body, laterally partially divided but only ventrally, hindwing twice as long as elytra, venation reduced, but at least one crossvein present, *Sc* and *R* fusing with the costa before the apex of the elytra to form a strong, much thickened vein; venation similar to that of *Nephrites* but *Cu* straighter after the crossvein, which is incomplete anteriorly, and 2*A* and the crossvein to 1*A* indistinct.

Type.—Holotype ♂ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Tidbinbilla, A.C.T. (13.x.1950, H. M. Cane).

Host.—Bred from an undescribed genus of cockroach belonging to the Pseudomopinae.

NEONEPHRITES MOLLIPES (Lea)

Rhipidius mollipes Lea, 1917, Trans. Roy. Soc. S. Aust. 41: 253.

The species is redescribed from the holotype.

Male

Reddish yellow, the head black, the elytra slightly darkened at apex and the flabellae of the antenna slightly darkened in the middle, palps dark brown.

Maxillary palps well developed, 3-segmented, the 1st longest, 2nd slightly shorter, 3rd half the 1st; head truncate posteriorly, from above wider than long, not produced anteriorly between the antennae but faintly excavate; eyes very large, almost reaching the caudal margin laterally and ventrally, touching over only a short distance dorsally, upper posterior margin almost straight, anterior margin deeply excised around the antenna; antenna 11-segmented, 1st segment large, expanding markedly to the apex, somewhat longer than its greatest width, 2nd and 3rd subequal, only about half as long as wide, 4-11 laterally strongly flabellate; hind tarsus 4-segmented, 1st segment largest, as long as the 2nd and 3rd combined, 3rd somewhat shorter than 2nd, 4th about twice the 3rd, fore and middle tarsi damaged on holotype, apparently 5-segmented; pronotum densely punctate and hirsute; prescutum raised at meson caudally, semicircular over posterior half, openly excavate over most of dorsal surface; thorax partly obscured by elytra and hindwings; scutellum produced at meson caudally to slightly overhang the postscutellar region, scutellum wide at anterior margin, as wide as the caudal half of the prescutum; elytra extending well over the abdomen, separated at bases by the width of the scutellum anteriorly, not their own width apart, apex rounded; hindwings folded, venation obscured.

Type.—Holotype ♂ in the South Australian Museum, carded specimen.

Type locality.—Kuranda, Qld. (Lea).

Only the holotype is known. The species can be separated readily from *partiniger* on colour.

Genus NEORHIPIDIUS, gen. nov.

Genotype *Neorhipidius neoxenus*, sp. nov.

Female

Body with head and portion of thorax sclerotized; antennae long, about 3 times the length of the palps, widely separated at the base, 11-segmented, segments 3-10 almost as long as wide, 9 and 10 somewhat produced, others less so, 11th obliquely produced, clubbed; head strongly dorsoventrally compressed, narrowly rectangular in lateral view, dorsal surface flat, strongly contracted posteriorly and with a very narrow attachment to the prothorax; mouth-parts reduced, but maxillary palps large, circular in cross section, inflated, 1st segment the largest, 2nd more than half the 1st, widest in the middle, narrowed to base and apex, 3rd half as long and wide as 2nd, narrowed at base, apex rounded, 1st segment widest towards the apex, narrowed at base; eye reduced, more than half as wide as long, with enlarged facets posteriorly, one very obviously so; no obvious frontal projection between the antennae; tibiae without apical spurs, upper surface smooth, but setose; all tarsi 4-segmented, elongate, 1st segment distinctly longer than wide, 2nd and 3rd decreasing, apical segment longest, twice the 1st segment in the hind tarsus.

In tarsal structure this genus is broadly similar to *Rhipidioides*, the tarsi being isomerous, but in other characters it is quite distinct. The palps are well developed, antennae distinctly 11-segmented, and the thorax partly sclerotized.

NEORHIPIDIUS NEOXENUS, sp. nov.

Plate 1, Figs. 9-11; Plate 2, Fig. 3

Female

Length 9 mm; colour of sclerotized portion black, abdomen with mottled grey appearance.

Head very small and strongly flattened above, about half the width of the pronotum, much longer than deep in lateral view, eye small, dorsoventrally elongate, considerably longer than the antennal insertion, more than half as wide as long; antennae inserted widely apart, 11-segmented, 1st segment much the largest, clubbed at apex, 2nd and succeeding segments almost quadrate, somewhat narrower at base than apex, apical segments somewhat produced, more noticeably 9th and 10th, 11th laterally produced, clubbed; maxillary palpi expanded, bulbous, together not much more than half as wide as the head, 1st segment largest, 2nd about half 1st, and 3rd about half 2nd and with rounded apex, 1st widest towards the apex and not at base; pronotum strongly arched, expanding rapidly posteriorly, posterior margin gently convex, lateral margin rounded, projecting lateral portion distinct, posteriorly slightly emarginate; meso- and metanota of increasing size, with both anterior and posterior margins almost straight, lateral projections decreasing in size; surface of all nota punctate and setose; abdominal segments decreasing regularly in size, 8th and succeeding partially hidden; prosternum sclerotized in part across the meson, mesosternum with a narrower sclerotized area; legs short, trochanters subequal, femora expanded in the middle, particularly fore and middle, fore and middle tibiae clubbed at apices, tarsi rather long, 1st segment longer than wide, segments decreasing regularly in length except that the apical is much the longest, tarsal claws simple, slightly flattened at base.

Type.—Holotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Canberra, A.C.T. (23.iv.1951, E. F. Riek).

Host.—Bred from the cockroach *Escala longiuscula* or *E. cucumducta* (subfamily Pseudomopinae) collected in the field 8.iii.1951. Only the holotype is known.

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EXPLANATION OF PLATES 1-4

PLATE 1

Fig. 1.—*Rhipidioides rubricatus*, gen. et sp. nov., holotype male. × *c.* 6.

Fig. 2.—*Rhipidioides helenae*, gen. et sp. nov., holotype male. × *c.* 6.

Fig. 3.—*Nephrites nitidus* Shuckard, male from Hobart. × *c.* 6.

Fig. 4.—*Nephrites nitidus* Shuckard, dried female from Hobart. × *c.* 6.

Fig. 5.—*Neonephrites partiniger*, gen. et sp. nov., holotype male. × *c.* 6.

Figs. 6-8.—*Rhipidioides helenae*, gen. et sp. nov., fore, middle, and hind legs, without coxae, of allotype female.

Figs. 9-11.—*Neorhipidius neoxenus*, gen. et sp. nov., fore, middle, and hind legs, of holotype female.

PLATE 2

Fig. 1.—*Nephrites australis*, sp. nov., holotype female, lateral view. × *c.* 4.

Fig. 2.—*Nephrites australis*, sp. nov., holotype female, ventral view. × *c.* 4.

Fig. 3.—*Neorhipidius neoxenus*, gen. et sp. nov., holotype female. × *c.* 4.

Fig. 4.—*Rhipidioides helenae*, gen. et sp. nov., allotype female, dorsal view. × *c.* 4.

Fig. 5.—*Rhipidioides helenae*, gen. et sp. nov., allotype female, lateral view. × *c.* 4.

Fig. 6.—*Rhipidioides helenae*, gen. et sp. nov., allotype female, ventral view. × *c.* 4.

Figs. 7 and 8.—*Rhipidioides* sp., larval parasite from cockroach *Escala longiuscula*, lateral and dorsal views. × *c.* 4.

PLATE 3

Figs. 1-3.—*Nephrites nitidus* Shuckard, from life, enlarged.

PLATE 4

Fig. 1.—*Nephrites* sp. from *Platyzosteria castanea* at Canberra, female pupa, ventral view. × *c.* 4.

Fig. 2.—*Nephrites nitidus* Shuckard, female pupa, lateral view. × *c.* 4.

Fig. 3.—*Nephrites nitidus* Shuckard, empty female pupa and egg-mass. × *c.* 4.

Fig. 4.—*Nephrites nitidus* Shuckard, male pupa, lateral view. × *c.* 6.

Fig. 5.—*Rhipidioides rubricatus*, gen. et sp. nov., male pupa, ventral view. × *c.* 6.

Fig. 6.—*Rhipidioides helenae*, gen. et sp. nov., female pupa, ventral view. × *c.* 6.

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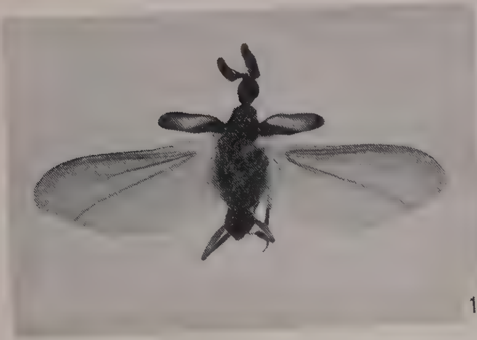
AUSTRALIAN RHIPIDIINE PARASITES OF COCKROACHES



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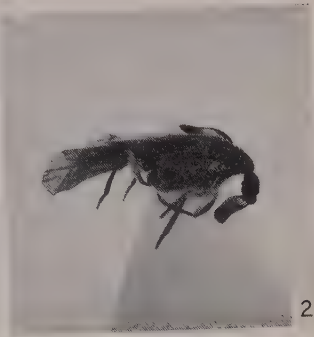

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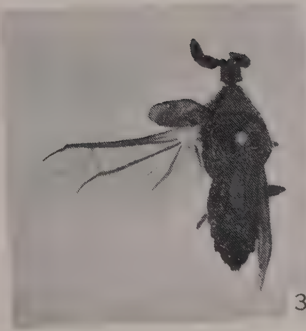

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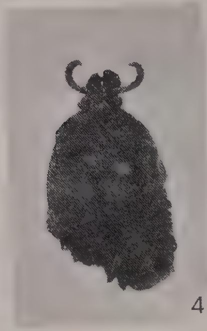

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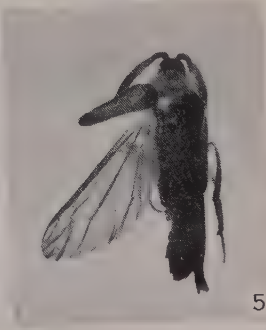

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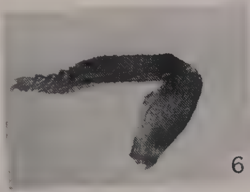

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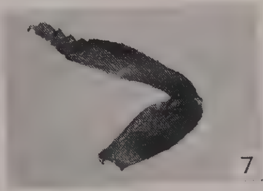

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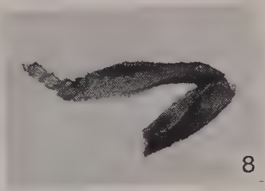

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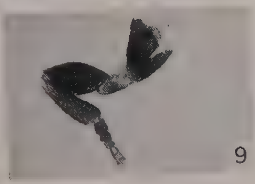

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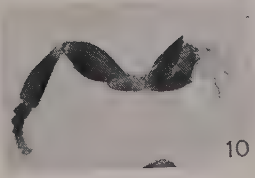

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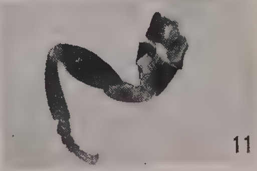

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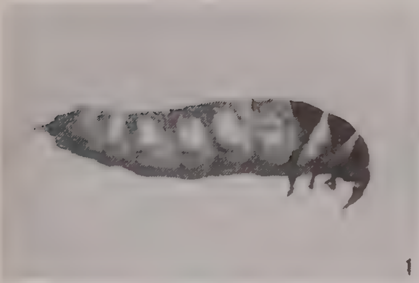
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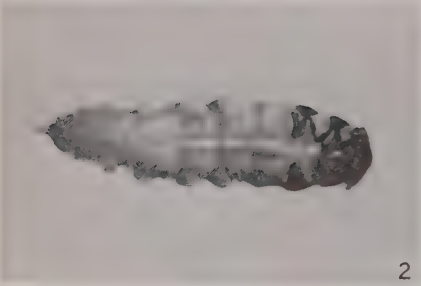
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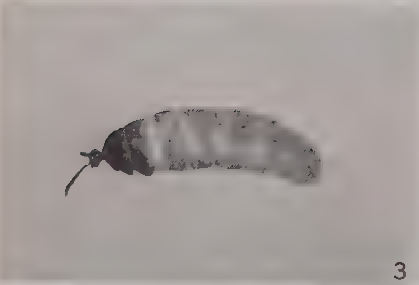
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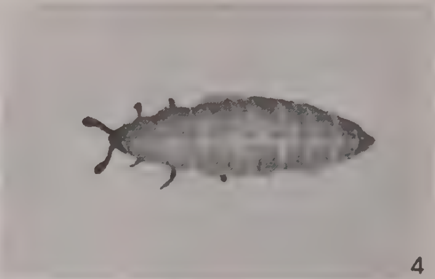
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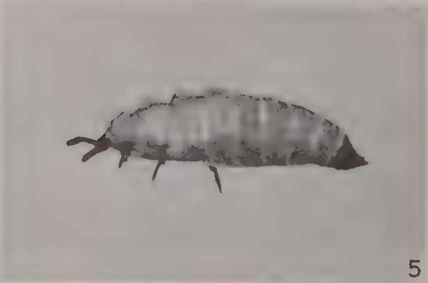
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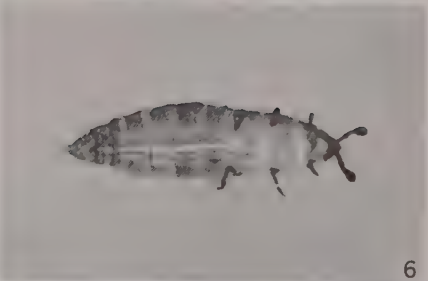
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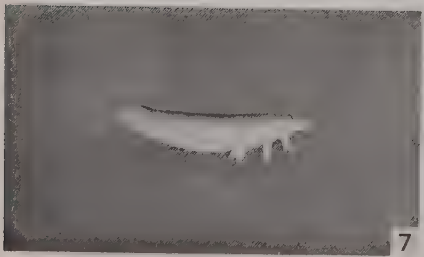
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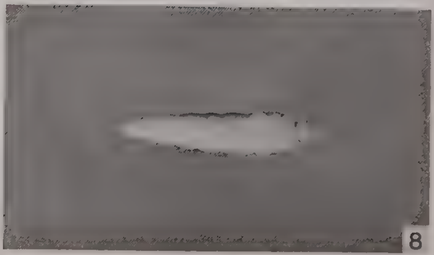
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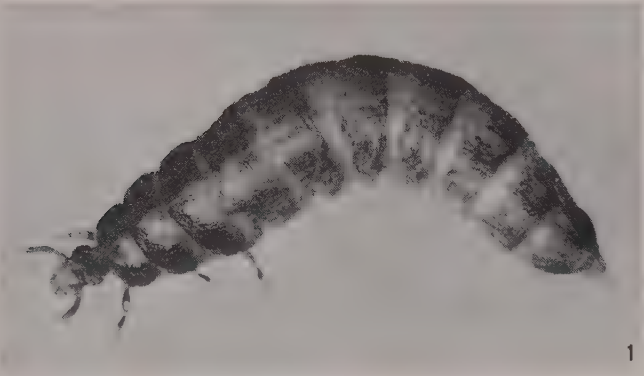

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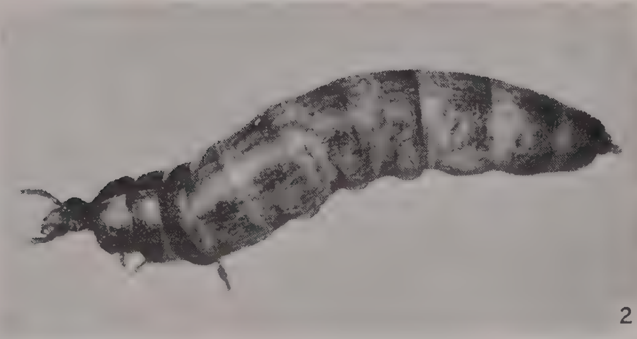

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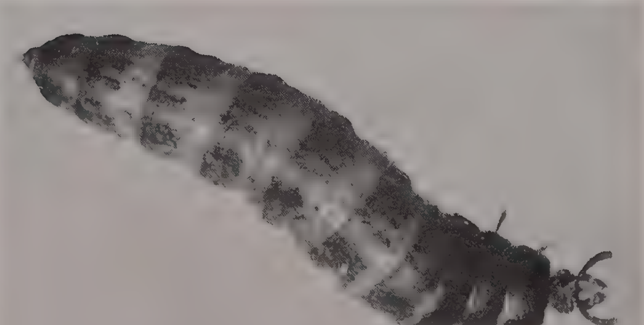

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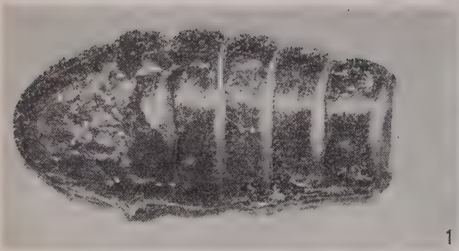

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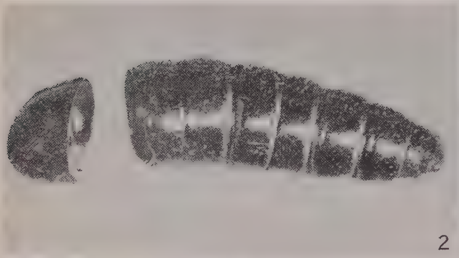

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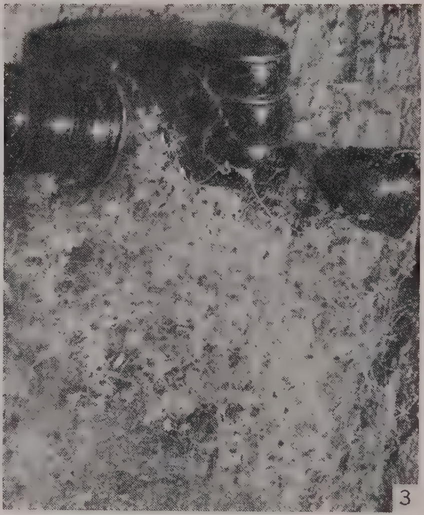

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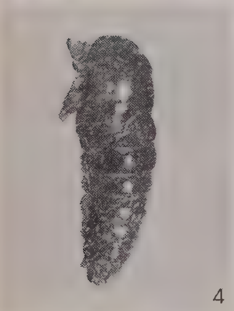

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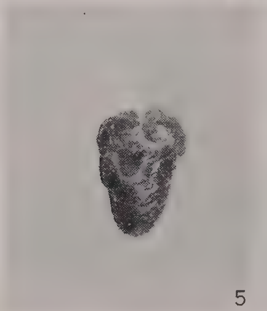

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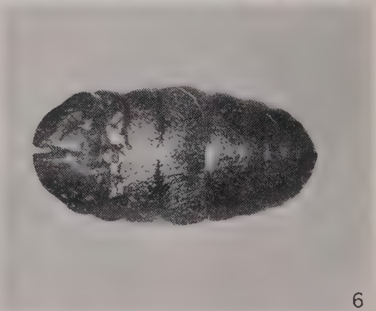

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AUSTRALIAN LEAF-MINING SAWFLIES OF THE GENUS *PHYLACTEOPHAGA* (HYMENOPTERA: TENTHREDINIDAE)

By E. F. RIEK*

(*Manuscript received June 23, 1954*)

Summary

A new species and a new subspecies of *Phylacteophaga* are described and the range of the previously known species extended.

INTRODUCTION

Froggatt (1899) described *Phylacteophaga eucalypti* from material bred from mines in *Eucalyptus globulus* collected at Melbourne, Vic. This is the only record of a sawfly mining eucalypt leaves but there are two other leaf-mining sawflies in Australia: *Zenarge turneri* Rohwer, a needle-miner of cypress pine, and *Trichorhachus australis* Westwood, a leaf-miner of pigweed.

Since the original record, *Phylacteophaga* has been bred from various eucalypts in Victoria, New South Wales, Queensland, and possibly Tasmania. Froggatt gave notes on all stages of *eucalypti* except the early larva. The control of these sawflies is important in nurseries and in ornamental plantings.

In the region of Canberra, A.C.T., there appear to be only two broods a year but on coastal New South Wales there is more overlapping of generations. At Canberra, adults of the autumn brood emerge generally in February and March, with a few in January. They are fairly heavily parasitized by a braconid and chalcidoid (eulophid) but they are still present in such numbers as to cause considerable damage to the young growth of the eucalypts. There is only one braconid parasite per host but up to eight or 10 eulophids emerge from the one *Phylacteophaga* mine. The braconid has almost the reverse colouring to that of the sawfly, having the propodeum and the abdomen, except narrowly at apex, reddish. The spring brood of the *Phylacteophaga* emerges in September and October and is more intensely coloured than is the autumn brood.

The form occurring on coastal New South Wales and Queensland differs quite markedly in colouring from the typical and is considered as a distinct species. Specimens from Tasmania differ less from the typical and are described as a subspecies of *eucalypti*.

Genus PHYLACTEOPHAGA Froggatt

Phylacteophaga Froggatt, 1899, Proc. Linn. Soc. N.S.W. 1899: 131.

Genotype *Phylacteophaga eucalypti* Froggatt, 1899, loc. cit. (original designation).

The genus, as erected by Froggatt, was monotypic.

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* Division of Entomology, C.S.I.R.O., Canberra, A.C.T.

KEY TO SPECIES OF THE GENUS PHYLACTEOPHAGA

Females

1. Scutellum darkened at least in part; antenna with scape and pedicel black; middle and hind legs mostly or all dark, fore leg all or mostly red........2
   Scutellum all pale; antenna with scape and pedicel reddish; legs, including coxae, all pale but apical segment of hind tarsus darkened.............. *froggatti*, sp. nov.
2. At least middle tibia pale below; middle tarsus pale over basal segments; fore leg all red. (Victoria and A.C.T.)...........*eucalypti eucalypti* Froggatt
   Middle and hind legs all dark; fore leg with tibia and tarsus slightly darkened (Tasmania)...........................*eucalypti tasmanica*, subsp. nov.

Males

Scape and pedicel pale; legs, except apex of hind tibia and all tarsus, pale; lateral thorax widely pale...........................*froggatti*, sp. nov.
Scape and pedicel black; at least hind coxa, apex of femur, tibia above and tarsus dark; lateral thorax all dark, except possibly below tegula........ *eucalypti eucalypti* Froggatt

PHYLACTEOPHAGA EUCALYPTI Froggatt

Plate 1, Figs. 1-5

Phylacteophaga eucalypti Froggatt, 1899, Proc. Linn. Soc. N.S.W. 1899: 131.

Froggatt described this species from larval and pupal stages as well as adult males and females. The adults are re-described below.

Female

Body black, marked with red. Head except antennae, anterior half of thorax, including axillae dorsally but running obliquely forward laterally, and all fore legs, red. Middle and hind legs with at least middle tibia pale below, usually hind tibia too; trochanters pale; middle tarsus pale. Scutellum black, at least at apex. Teeth of mandibles somewhat darkened. Antenna pale at base of funicle, dark at apex. Otherwise body black. Ovipositor valves all black.

Male

With considerably more black than female. Thorax all black except for tegula, and sometimes a spot below tegula (posterolateral pronotum and anterodorsal mesopleuron). Head all red except for black at vertex surrounding the ocelli. Antenna dark but pale below at basal funicle. Mandibles with teeth darkened at apex. Fore legs all pale. Middle and hind legs variable but hind leg with at least coxa, apex femur, tibia except below, and tarsus, except apical segment, dark. Middle leg with tibia and tarsus pale. Apical segments of abdomen pale below or all dark.

Types.—There are two card mounted males labelled "French, Vic. 28-2-99" and a similarly mounted female and male, in the Froggatt collection, Division of Entomology, C.S.I.R.O., Canberra. All are somewhat damaged. These appear to be at least paratypes. The location of the holotype is not known.

Type locality.—Melbourne, Vic. (coll. C. French) reared from mines in *Eucalyptus globulus.*

The species has been bred in considerable numbers from leaf mines on *E. globulus* and other eucalypts planted at Canberra, A.C.T. (Feb. and Sept. 1952, E. F. Riek). Also from *E. grandis,* Arboretum, Cotter Road, Canberra (18.x.1950, I. F. B. Common) 1 ♂.

Female specimens of the spring generation all have the hind tibia all dark and the first funicle segment all dark.

PHYLACTEOPHAGA EUCALYPTI TASMANICA, subsp. nov.

Female

Similar to the typical form but apical 4 segments of antenna pale or dark, and funicle segments dark to base. Forelegs mostly red but tibia and tarsus brownish; middle and hind legs, including trochanters, all dark. Apical 2 segments of the abdomen pale but ovipositor valves mostly dark as in the typical form. Vertex of head slightly darkened at ocelli. Ovipositor valves narrowly pale at base.

Male

Unknown.

Type.—Holotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Boat Harbour, St. Helens, Tas. (11.i.1949, E. F. Riek), apparently from leaf mines on *Acacia sophorae,* 1 ♀. There is a possibility of contamination and the host plant may have been a *Eucalyptus* species as in all other known cases.

There is a male in the Division of Entomology Museum, C.S.I.R.O., from the summit of Mt. Wellington, Tas. (Dec. 1902, Lea), which may be the male of this subspecies. It differs from the male of *eucalypti eucalypti* mainly in the colour of the legs. Middle and hind legs all dark except apex of femur and base of tibia narrowly and apical segment of tarsus (but less so); fore leg darkened at coxa, trochanter, about basal half of femur, and less so apex of tibia.

PHYLACTEOPHAGA FROGGATTI, sp. nov.

Plate 1, Fig. 6

Female

Body black and red, with considerably more red than in *eucalypti.* Head red except for antennae, thorax red except for propodeum and small areas on lateral and ventral thorax. Abdomen all dark or apical 3 segments pale in part. Legs, including coxae, all pale but apical segment of hind tarsus darkened. Teeth of mandibles generally all pale. Antenna with scape and pedicel pale, reddish, basal funicle pale, remainder brownish. Ovipositor valves pale at least at base.

Male

With more black than in female but paler than male *eucalypti*. Thorax above all black except for tegula. Lateral thorax partly widely reddish, particularly prothorax. Legs, except apex of hind tibia and all tarsus, pale. Abdomen with apical segment pale below. Head all red except at vertex surrounding ocelli. Antenna with scape and pedicel pale, funicle pale, at least below.

Types.—Holotype ♀, allotype ♂, and a long series of paratypes in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Schofields, N.S.W. (6.ii.1953, P. Hadlington) 77 ♀♀, 19 ♂♂. Paratypes also from East Lindfield, N.S.W. (18.i.1953, P. Hadlington) 7 ♀♀, 4 ♂♂, and Sandringham, N.S.W. (14.ii.1953, P. Hadlington) 26 ♀♀, 5 ♂♂.

The species is recorded also from NEW SOUTH WALES: Lismore (10.xii.1903, W. W. Froggatt); Sydney ? (9.iii.1953), many ♂♂, ♀♀ in N.S.W. Dep. Agric. Ent. coll. QUEENSLAND: Crows Nest (Sept. 1920) 5 ♀♀, 1 ♂ in Queensland Museum, Brisbane; Brisbane (18.ix.1935, A. R. Brimblecombe) several ♂♂, ♀♀ in Queensland Dep. Agric., Entomology Branch collection.

The species is distinctly more red than *eucalypti*. The scape and pedicel and fore and middle legs are pale in both sexes whereas in *eucalypti* the scape and pedicel are all dark in both sexes, and the middle leg is mostly dark in the female.

REFERENCE

FROGGATT, W. W. (1899).—A new genus and species of sawfly. *Proc. Linn. Soc. N.S.W.* 1899: 130-4.

EXPLANATION OF PLATE 1

Figs. 1-5.—*Phylacteophaga eucalypti* Froggatt.

Fig. 1.—Leaf-mine showing in outline the enclosed pupa and emergence hole of adult. × *c.* 1.5.

Fig. 2.—Leaf-mine showing emergence hole of braconid parasite. × *c.* 1.5.

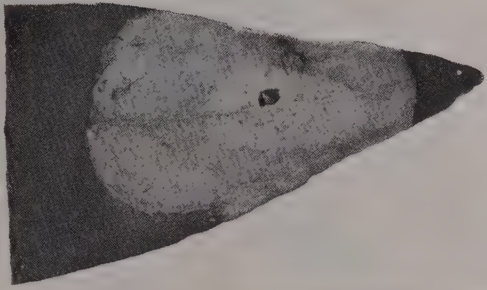
Fig. 3.—Leaf-mine showing emergence hole of chalcidoid parasites. × *c.* 1.5.

Fig. 4.—Female. × *c.* 5.

Fig. 5.—Male. × *c.* 5.

Fig. 6.—*Phylacteophaga froggatti*, sp. nov., mature larva. × *c.* 10.

AUSTRALIAN SAWFLIES, GENUS PHYLACTEOPHAGA



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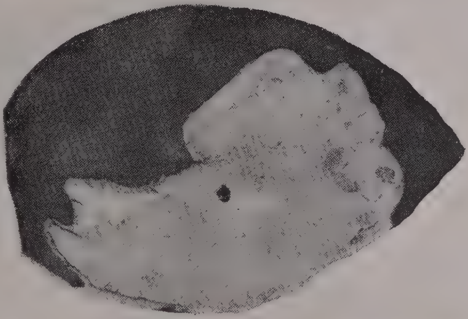

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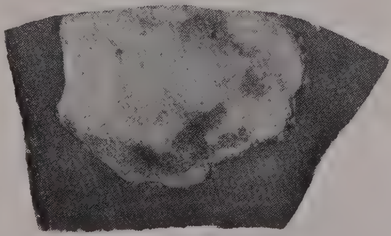

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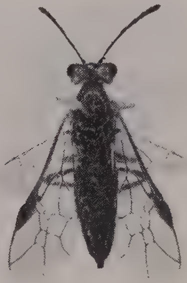

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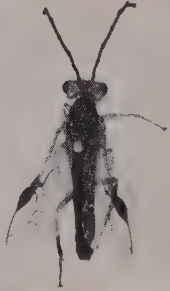

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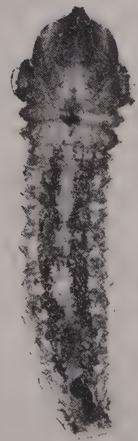

6

THE AUSTRALIAN SAWFLIES OF THE FAMILY ORUSSIDAE (HYMENOPTERA: SYMPHYTA)

By E. F. RIEK*

(*Manuscript received June 23, 1954*)

Summary

The paper deals with the systematics of the Australian representatives of this small family of sawflies. A most distinctive new genus and a new species of *Guiglia* are described. Revised keys to the species of *Guiglia* and *Orussobaius* are given.

INTRODUCTION

These rare insects are characterized by the insertion of the antennae on the ventral aspect of the head, below the apparent clypeus and below the lower margins of the eyes; antenna 11-segmented in the male but in the female only 10-segmented and with the penultimate segment distinctive, swollen and longer than any other segment; pronotum strongly emarginate behind; wing venation reduced mostly to pigmented bands, only one interradial crossvein in the forewing and no crossveins *r-m* or *m-cu* in the hindwing; female saw-sheath exserted.

The larvae, as far as is known, are unique among the sawflies in that they are internal parasites of wood-boring beetle larvae (Buprestidae). Little is known of the life histories of the Australian species but *Orussobaius wilsoni* Benson may possibly be a parasite of *Melobasis purpurescens* Fabricius, a buprestid attacking acacias.

The general morphology of the group has been dealt with by Rohwer (1912). Benson (1938*b*) recorded six species of two genera from Australia but through synonymy only five of these are recognized in this paper. A new species of *Guiglia* is described, while another species, with a peculiar dorsoventrally compressed body and a head which appears prognathous, is considered in a new genus.

KEY TO AUSTRALIAN GENERA OF THE FAMILY ORUSSIDAE

1. Frontal area without carinae between the eyes; apical spurs of hind tibia almost equal in length..2

Frontal area with 2 diverging longitudinal carinae between the eyes; inner spur at apex of hind tibia about half the length of the outer one.......... *Guiglia* Benson

2. Body strongly dorsoventrally compressed, head appearing prognathous, the caudal margin of the head strongly excavated; hind femur not markedly swollen, almost 3 times as long as wide; lateral margins of abdominal segments, at least 3-6, carinate......................*Orussonia*, **gen. nov.**

Body normal, head hypognathous; hind femur strongly swollen, less than 3 times as long as wide; lateral margins of abdominal segments not carinate, except possibly 1-2................................*Orussobaius* Benson

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Genus ORUSSOBAIUS Benson

Orussobaius Benson, 1938, Ann. Mag. Nat. Hist. (11) 2: 9.

Genotype *Orussobaius mesembrinus* Benson, 1938, loc. cit. (original designation).

Head without carinae on the face between the eyes, front marginal carina to frontal area absent or at least broken in the middle; female with antennal segments 4 and 5 not much shortened, 3 and 4 almost equal, in the male 4 is longer than 3; maxillary palp 5- and labial palp 3-segmented; 2 pairs of tubercles beside the median ocellus and behind the ocellus transverse ridges to represent 3 other pairs fused; in the forewing the basal vein joins the cubitus some distance from the subcosta, so that the discoidal cell is petiolate; discoidal cell with base and apex of about equal breadth; hind femur swollen strongly, less than 2½ times as long as broad; apical spurs of hind tibia almost equal in length; 2nd abdominal tergite almost equal to 3rd and 4th together.

Adults are taken on wattle trees (*Acacia* spp.).

KEY TO SPECIES OF THE GENUS ORUSSOBAIUS

1. Scutellum coarsely punctured, with shining interspaces....................2
   Scutellum dull, with very dense and fine sculpture, without shining interspaces; (hind tibia with 2 rows of teeth on the upper side)........*wilsoni* Benson
2. Hind tibia with 2 rows of teeth on the upper side; hind femur at least half as broad as long; hind tibial spurs shorter than half the apical breadth of the tibia; length 3-7 mm................................*minutus* Benson
   Hind tibia without definite teeth on the upper side; hind femur only about three-eighths as broad as long; hind tibial spurs longer than half the apical breadth of the tibia; length 7.5-11 mm............*mesembrinus* Benson

ORUSSOBAIUS MESEMBRINUS Benson

Orussobaius mesembrinus Benson, 1938, Ann. Mag. Nat. Hist. (11) 2: 9.

Types.—Holotype ♀, allotype ♂ in F. E. Wilson collection, Melbourne, paratype ♀ in the British Museum.

Type locality.—Bogan River, N.S.W. (Oct. 1932, J. Armstrong). Allotype male examined.

ORUSSOBAIUS MINUTUS Benson

Orussobaius minutus Benson, 1938, Ann. Mag. Nat. Hist. (11) 2: 10.

The holotype shows 2 rows of distinct teeth on the upper side of the hind tibia but in both cases they are partly obscured by the wings, which are glued over them.

Types.—Holotype ♀ and paratype ♂ in F. E. Wilson collection, Melbourne, allotype ♂ in the British Museum.

Type locality.—Bogan River, N.S.W. (J. Armstrong).

Specimens examined.—A much larger female (7 mm) from Grandchester, Qld. (1.viii.1924, A. A. Girault) and a male from Gympie, Qld.

(A. A. Girault) have been examined in addition to the types in the F. E. Wilson collection.

ORUSSOBAIUS WILSONI Benson

Plate 2, Fig. 1

Orussobaius wilsoni Benson, 1938, Ann. Mag. Nat. Hist. (11) 2: 10.

Orussobaius normani Rayment, 1951, Vict. Nat. 68: 113.

Only the female was described by Benson.

Male

Differs slightly from female. Pronotum all dark; not piceous in part as in the female. Only the 2 apical fuscous bands are present in the forewing and these are paler than in female; pterostigma black with a fuscous margin, venation brown, particularly *R* and *CuA;* punctures of the scutellum very little finer than those of the scutum.

Types.—Holotype ♀ in F. E. Wilson collection, Melbourne, allotype ♂ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Holotype, Ferntree Gully, Vic. (8.iii.1931, F. E. Wilson); allotype, Sunnybank, Qld. (18.ix.1927, F. A. Perkins).

The types of *normani* Rayment from Lane Cove, N.S.W. (4.x.1947, N. W. Rodd) are in the Rayment collection, Melbourne.

The wing pigmentation pattern, even of the male, is very distinct in this species. The holotype has been examined but not the types of *normani.* Rayment did not examine the types in the F. E. Wilson collection before describing *normani* but his description fits that of the type specimens.

Genus GUIGLIA Benson

Guiglia Benson, 1938, Ann. Mag. Nat. Hist. (11) 2: 13.

Genotype *Guiglia bombycinis* Benson, 1938, loc. cit. (original designation).

Head with the frontal area surrounded by carinae, a pair of carinae on the inner orbits which diverge towards the front, these are joined in front by a transverse carina immediately above the antennae, and generally behind by a transverse carina in front of the anterior ocellus; female with antennal segments 4 and 5 not much shortened, 3 and 4 of almost equal length; maxillary palp 5- and labial palp 3-segmented; 4 or 5 pairs of tubercles in the ocellar region; in the forewing the basal vein joins the cubitus some distance from the subcosta so that the discoidal cell is petiolate; discoidal cell with base and apex of equal breadth, hind femur at least 3 times as long as broad; inner spur at apex of hind tibia about half length of outer one; 2nd abdominal tergite less than 3rd and 4th together (in the middle).

Adults are taken on eucalypt trees.

KEY TO SPECIES OF THE GENUS GUIGLIA

1. Carinated frontal area longer than broad; dense setae on abdominal segments 7 and 8; female forewing with 3 hyaline bands........................2
   Carinated frontal area about as broad as long; conspicuous dense setae on abdominal segments 6-8; female forewing with 2 hyaline bands............ *sericatus* (Mocsáry)
2. Female with thorax distinctly partly red, legs all red except coxae and fore tibia in part (black) and base of hind tibia (white) and apical segment of tarsi (black); male thorax all black, legs all red except coxae in part (black) and bases of tibiae (white) and black apical segments of tarsi; apical dark band of forewing almost quadrate............*rubricata*, sp. nov.
   Female with thorax touched with reddish brown, legs red except black bases of coxae and white outer side and base of hind tibia; male legs black or darkened except joints, bases of tibiae widely, particularly hind; apical dark band of forewing not as wide as width of wing........*bombycinis* Benson

GUIGLIA BOMBYCINIS Benson

Guiglia bombycinis Benson, 1938, Ann. Mag. Nat. Hist. (11) 2: 13.
Guiglia sericata Maa, 1950 part, Proc. R. Ent. Soc. Lond. B 19: 33.

Benson described both sexes. The species can be distinguished on the shape of the face, ornamentation of the hind tibia, and colour.

Types.—Holotype ♀, allotype ♂, and paratypes in the British Museum.

Type locality.—Kuranda, Qld. (4-29.vii.1913, R. E. Turner) 1100 ft.

Specimens examined.—There is a topotypical paratype ♀ in the South Australian Museum, Adelaide, paratype ♂ in the Division of Entomology Museum, C.S.I.R.O., Canberra, paratype ♂ in National Museum, Melbourne, a paratype ♀ and a ♂ from the type locality in the Queensland Museum, Brisbane.

The description of the allotype male of *sericata* described by Maa fits that of a paratype male of *bombycinis* Benson in the Division of Entomology Museum, C.S.I.R.O. Benson did not give a very full colour description but the shape of the carinated frontal area and the spines of the hind tibia are distinctive. This frontal area has the upper transverse carina more angulated at the meson in the male than is figured by Benson.

GUIGLIA SERICATUS (Mocsáry)

Ophrynopus sericatus Mocsáry, 1900, Termes Fuzet. 23: 126.
Oryssus queenslandensis G. Turner, 1900, Proc. Linn. Soc. N.S.W. 25: 514.
Guiglia sericatus Benson, 1938, Ann. Mag. Nat. Hist. (11) 2: 14.
Guiglia queenslandensis Benson, 1938, Ann. Mag. Nat. Hist. (11) 2: 14.
Guiglia queenslandensis coronatus Rayment, 1951, Vict. Nat. 68: 111.

There is a damaged female specimen from Mackay (Aug. 1899) and a fine female specimen bred from a beetle larva at Sydney (16.x.1924, W. W. Froggatt) in the Froggatt collection. These two specimens are conspecific. It is considered that *queenslandensis* Turner is a synonym of *sericatus* Mocsáry and not distinct as inferred by Benson. The holotype of *queenslandensis* is in the British Museum. The specimen examined from Mackay may possibly be the second one referred to by Turner in his description of *queenslandensis*. There is a female specimen from the S. Johnstone River, Qld. (H. W. Brown) determined as *queenslandensis* by Benson in 1938 in the South Australian Museum. There is a male from National Park, Qld. (December 1919, H. Hacker) in the Queensland Museum. Also one male, Hamilton, Vic. (18.xii.1947, G. Stephens) in the Burns collection. Recently, Rayment has re-described both sexes from Fraser Park, N.S.W. as a distinct subspecies. Maa (1950) designated an allotype male but the specimen is considered to be a male of *bombycinis* Benson.

GUIGLIA RUBRICATA, sp. nov.

Plate 1, Figs. 1 and 2

Structurally very similar to *bombycinis* Benson but differing in coloration of body, legs, and wings. There is some variation in the row of dorsal teeth on the hind tibia but in this character the species also approaches *bombycinis*.

Female

Head and abdomen black, thorax widely red; scutum except at meson anteriorly, parapside, scutellum, axilla, postscutellum at meson narrowly, red, thorax laterally all red, except prothorax in part; legs mostly red, coxae in part, apical segment of all tarsi and fore tibia at middle third, black, apices of femora and bases of tibiae, especially hind tibia, white; tegula red; antenna all dark; apical dark band of forewing almost quadrate, extending basad almost to the middle of the stigma, apical portion of stigma black.

Hind tibia with a single row of teeth on the upper side or with an additional tooth on the mesal side of this row at the apex (variable on the 2 legs of the holotype).

Male

Body all black; legs red except black coxae in part and apical segment of tarsi and white base of hind tibia; apical dark band of forewing not quite quadrate, extending basad only to the apical third of the stigma, apical portion of stigma black.

Hind tibia with a 2nd row of 2 or 3 weak teeth on the mesal side of the main row and towards the apex.

Types.—Holotype ♀, allotype ♂, and paratypes in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Eight miles E. of Braidwood, N.S.W. (25.xi.1952, E. F. Riek).

Locality records.—NEW SOUTH WALES: Monga (19.xi.1952, E. F. Riek); 4 miles N. of Bateman's Bay (14, 21.x.1952, E. F. Riek).

The specimens were taken on the trunks of standing eucalypts, the females on dead trees and the males mostly on living smooth-barked trees. The males were only taken in direct sunlight.

Genus ORUSSONIA, gen. nov.

Genotype *Orussonia depressa*, sp. nov.

Male only, known. Body strongly dorsoventrally compressed; head appearing prognathous, the caudal margin of the head strongly excavated so that it fits around the pronotum; head without carinae on the face between the eyes; front marginal carina to the frontal area complete but slightly emarginate at meson; maxillary palp 5- and labial palp 3-segmented; 3 pairs of tubercles diverging from apex to level of the median ocellus; mesal margins of eyes straight and parallel; wing venation as in *Orussobaius;* hind femur not strongly swollen, almost 3 times as long as wide; apical spurs of hind tibia almost equal in length; scutellum in outline shaped as in *Orussobaius;* 2nd abdominal tergite almost equal to 3 plus 4; lateral margins of abdomen carinate, at least from 3 to 6.

ORUSSONIA DEPRESSA, sp. nov.

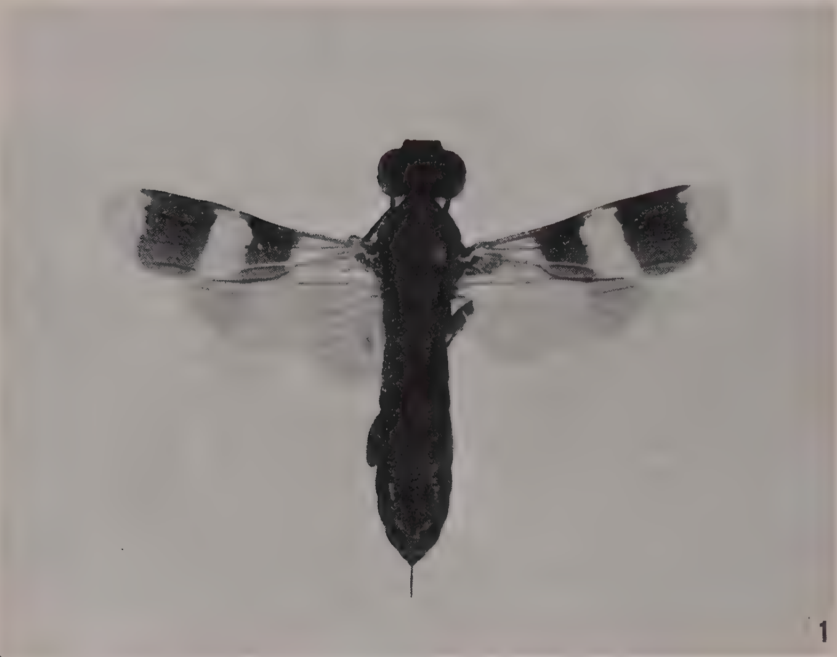
Plate 2, Figs. 2 and 3

Male

Body black; forewing infuscated from just beyond the stigma to the apex and a wide transverse band at the middle of the basal half; antenna dark, scape, pedicel (less so), and basal funicle red or reddish; legs dark, apices of all tibiae and dorsal two-thirds of hind tibia and all tarsi except apical segment red or reddish.

Ornamentation of body mostly fine; scutellum glabrous except for a few coarse shallow punctures; axillae meeting widely at meson and there with a raised carina; scutum with a low median carina, indistinct anteriorly, there tending to be glabrous; pronotum with the dorsal area almost linear; carinate behind, a single row of foveae extending over its surface, strongly carinate at junction of ventral and lateral surfaces; head with the area between the eyes plane except for tubercles at vertex, surface with scattered thimble-punctures, the area between glabrous laterad but finely punctate at meson widely, vertex and laterally irregularly foveate; abdominal tergites finely ornamented except for glabrous caudal margins, ornamentation transversely rugulose except laterally and there finely tuberculate, ornamentation of segments 1 and 2, particularly 1, coarser and more irregular; lateral margins of abdominal segments 3-6 carinate, less so 1, and 1 without distinct laterad carina parallel to the lateral margin; mesothorax laterally in part and hind coxa laterally with a patch of dense white hairs; hind tibia above with stout hairs but not clearly tuberculate; hind femur not markedly swollen, almost 3 times as long as wide.

AUSTRALIAN SAWFLIES, FAMILY ORUSSIDAE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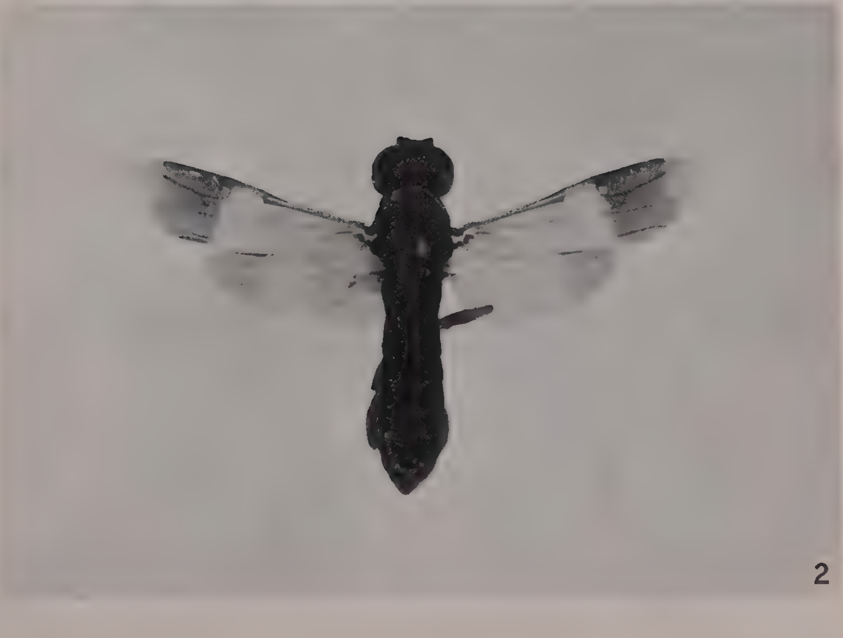
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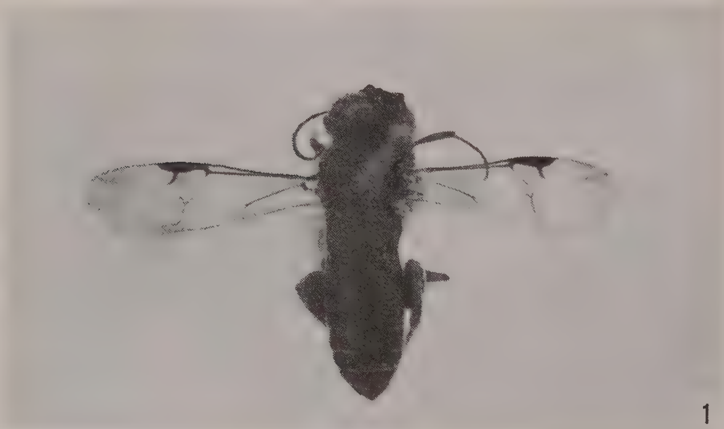
AUSTRALIAN SAWFLIES, FAMILY ORUSSIDAE



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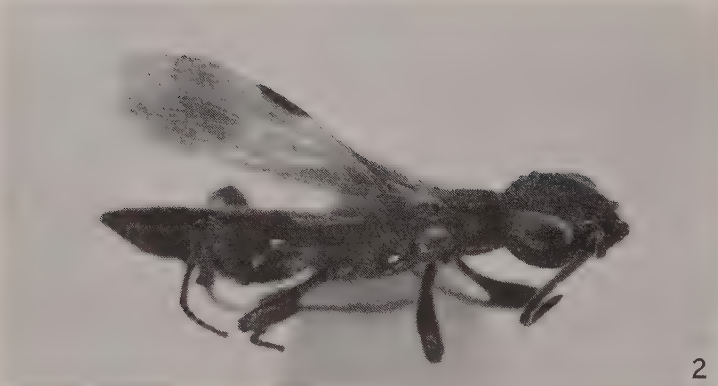

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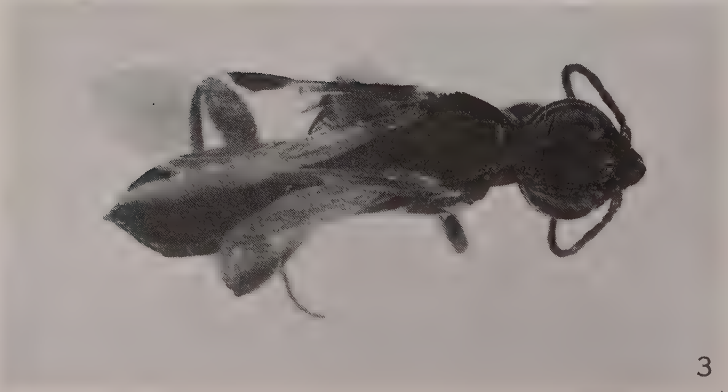

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Types.—Holotype ♂ and paratype ♂ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Four miles N. of Bateman's Bay, N.S.W. (14.x.1952, E. F. Riek).

The specimens were taken walking over the trunk of a living smooth-barked eucalypt in full sunshine. At first sight the specimens were mistaken for small ampulicids, mainly because of their distinctive head structure and flattened body.

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EXPLANATION OF PLATES 1 AND 2

PLATE 1

Fig. 1.—*Guiglia rubricata*, sp. nov., holotype female, × *c.* 6.
Fig. 2.—*Guiglia rubricata*, sp. nov., allotype male, × *c.* 6.

PLATE 2

Fig. 1.—*Orussobaius wilsoni* Benson, allotype male, × *c.* 9.
Fig. 2.—*Orussonia depressa*, gen. et sp. nov., holotype male, lateral, × *c.* 13.
Fig. 3.—*Orussonia depressa*, gen. et. sp. nov., holotype male, dorsal, × *c.* 13.

Genus AUSTROSERPHUS Dodd

Austroserphus Dodd, 1933, Proc. Linn. Soc. N.S.W. 58: 275.

Genotype *Austroserphus albofasciatus* Dodd, 1933, op. cit. 276 (original designation).

Venation very well developed, with 3 veins arising from the base in the forewing (*R*, *M + Cu*, 1*A + CuP*) and extending as distinct veins to the wing margin; scutum with parapsidal furrows percurrent, just touching caudally, scutum caudally with a sharp median carina, anteriorly with a pair of indistinct carinae; pronotum with distinct transverse carina at the declivity, with the posterolateral angle somewhat produced; propleuron not striate but with a single deep sulcus; scutellum with a deep transverse groove at base, subdivided by strong longitudinal carinae into 5 fovea; postscutellum only slightly produced at meson; petiole of abdomen distinct, longer than wide in both sexes; abdomen smooth at base; antenna 13-segmented, scape rather stout, its upper margin carinate, produced at apex dorsally into a large acute spine, covering the pedicel and base of 1st funicle; mandibles small, the teeth indistinct; fore trochanter distinctly 2-segmented, middle and hind only 1-segmented.

The very complete venation and divided trochanter of the fore leg distinguish this genus.

AUSTROSERPHUS ALBOFASCIATUS Dodd

Plate 1, Figs. 1-3

Austroserphus albofasciatus Dodd, 1933, Proc. Linn. Soc. N.S.W. 58: 276.

Female

Shining black; antenna mostly black except for white 9th and most of 10th segments of antenna, apex of 10th brownish; legs black except for white cinctus towards base of tibiae and white 3rd and 4th segments of middle and hind tarsi; fore tibia and tarsus with similar areas whitish; palps whitish.

Body shining, smooth, with scattered pin-punctures, the propodeum rugose except anteriorly; scutum and parapsides strongly convexed; propodeum smooth at basal third and with almost smooth patches posteriorly on either side of the median carina, otherwise rugose, irregularly produced posterolaterally, almost at anterior margin the propodeum bears 4 rounded teeth directed anteriorly, almost touching corresponding teeth directed caudally from the anterior margin of propodeum; abdominal petiole slightly longer than wide at base, glabrous widely at meson, carinate towards lateral margin, irregularly longitudinally carinate laterally; abdomen smooth at base, surface with scattered fine setae; forewing long, broad, slightly infuscated, venation fuscous; funicle segments long and slender, 1st longest, as long as scape, 10th funicle slightly more than half 1st, apical segment almost as long as 1st funicle, rounded at apex.

Male

Similar colouring to female.

First funicle a little longer than scape, apical segment three-quarters as long as 1st funicle, pointed at apex; petiole long and slender, 4 times as long as wide, with 2 median striae diverging somewhat at base and apex, laterally with a few strong, irregular, longitudinal striae.

Types.—Holotype, allotype, and paratype in the F. E. Wilson collection; one male and one female paratype in both the Queensland Museum and the Division of Entomology Museum, C.S.I.R.O., Canberra (ex Dodd collection).

Type locality.—Beech Forest, Vic. (Jan. 1932, F. E. Wilson).

Localities.—VICTORIA: Millgrove (November, F. E. Wilson). TASMANIA: Mt. Wellington (Lea), in Division of Entomology Museum, C.S.I.R.O., Canberra.

The two females and a male from Tasmania agree in all essential characters with the type series.

Genus ACANTHOSERPHUS Dodd

Acanthoserphus Dodd, 1915, Trans. Roy. Soc. S. Aust. 39: 384.

Genotype *Acanthoserphus albicoxa* Dodd, 1915, op. cit. 385 (original designation).

Venation relatively well developed, with 3 veins arising from the base in the forewing (R, $M + Cu$, $1A + CuP$); scutum with parapsidal furrows percurrent and with a median sulcus; pronotum with posterolateral angle produced into a strong dorsally projecting spine with apex flattened; propleuron not striate; scutellum with a deep transverse groove at base; postscutellum produced at meson into a long, backwardly curved projection, with rounded apex; petiole of abdomen very short; abdomen smooth at base; antenna 13-segmented, scape rather stout, produced at apex dorsally into an acute spine, covering the pedicel and base of 1st funicle; mandible small, appearing to be absent.

The form of the scape, apparent absence of mandibles, spined pronotum and postscutellum, slender pterostigma, and well-developed venation readily distinguish this genus.

ACANTHOSERPHUS ALBICOXA Dodd

Acanthoserphus albicoxa Dodd, 1915, Trans. Roy. Soc. S. Aust. 39: 385.

Female

Black, thorax mostly black, scutum and parapsides paler, abdomen as scutum; tegula yellowish; coxae all white, otherwise legs reddish; antenna mostly black, scape and pedicel golden yellow, segments 9 and 10, except at apex, white.

Body shining, smooth, with very scattered pin-punctures, the propodeum rugose but almost glabrous at meson, median carina indistinct; scutum and parapsides strongly convexed; abdomen smooth at base; forewing long, broad, uniformly, darkly infuscated, the venation fuscous; funicle segments long and slender, gradually shortening, the 1st longest, 10th not twice as long as wide, the apical segment one-third longer than preceding, broadly rounded at apex.

Male

Similar to female but pale areas of the thorax larger; funicle wholly black.

The 10th funicle segment 2½ times as long as wide, apical segment pointed at apex.

Types.—Holotype and allotype in the South Australian Museum. Specimens card-mounted, heads, antennae, and wings on a slide.

Type locality.—Kuranda, Qld. (3.iv.1915, A. P. Dodd), 1200 ft. Taken on decayed log in jungle.

Only the type specimens are known.

Genus DISOGMUS Foerster

Disogmus Foerster, 1856, Hym. Stud. **2**: 99.

Genotype *Proctotrupes areolator* Haliday, 1839, Hym. Brit. **1**: 13 (monobasic).

DISOGMUS NIGERRIMUS Dodd

Disogmus nigerrimus Dodd, 1915, Trans. Roy. Soc. S. Aust. **39**: 386.

Female

Shining black; tegula dark; legs dark, except joints, tarsi, and less so fore tibia.

Thorax convex dorsally; scutum and scutellum smooth, shining; parapsidal furrows deep and percurrent; propodeum with a deep transverse groove at base, interrupted at meson, with a median carina only over the caudal half, anteriorly irregularly foveate; propodeal spiracle raised; petiole visible as a transverse line; abdomen compressed laterally, somewhat narrowed at base, as long as the thorax, striate at base; ovipositor about as long as rest of abdomen; forewing long, broad, subhyaline but with a large, square blotch, commencing at base of pterostigma and continued some distance beyond the radial vein, extending fully half way across the wing, dusky; venation fuscous; pterostigma large, semicircular; radial cell small, not half as large as pterostigma; scape moderately long, pedicel short, wider than long; funicle segments long, filiform, 1st at least twice as long as wide, 10th a little shorter, apical somewhat longer.

Type.—Holotype ♀ in the South Australian Museum. Female on a card, head, antennae, and forewings on a slide.

Type locality.—Hobart, Tas. (A. M. Lea).

Only the holotype is known.

Genus PROCTOTRUPES Latreille

Proctotrupes Latreille, 1796, Précis Caract. Gen. Ins.: 108.

Genotype *Proctotrupes brevipennis* Latreille, 1802, Hist. Crust. Ins. 3: 307 (Int. Comm. Zool. Nomenc. Op. 178, 1946).

PROCTOTRUPES JANTHINAE (Dodd)

Proctotrypes janthinae Dodd, 1915, Trans. Roy. Soc. S. Aust. 39: 387.

Proctotrupes janthinae Dodd, 1920, Trans. Ent. Soc. Lond. 1919: 364.

Female

Shining black, antenna all black; legs black, paler at joints, tarsi, and basal half of hind tibia; fore tibia and tarsus golden yellow.

Head, scutum, and scutellum smooth, with fine pubescence; propleuron smooth, but with some striae; mesopleuron striate on dorsal half; parapsidal furrows completely absent; propodeum rugose, the anterior portion short at meson, the dividing carina thus V-shaped with its apex cephalad; petiole not visible from above; abdomen abruptly convex above from its base (in lateral view), produced into a long ovipositor, longer than the rest of the abdomen; forewing long, broad, hyaline; venation fuscous; pterostigma large, as wide as long, radial vein small, almost confluent with the pterostigma, radial cell very narrow; scape as long as 1st funicle, pedicel much wider than long, 1st funicle at least twice as long as wide, succeeding shortening, penultimate one-third longer than wide, apical segment distinctly longer than scape.

Type.—Holotype ♀ in the National Museum, Melbourne. The female on a card, antennae and forewings on a slide.

Type locality.—(? Melbourne), Vic. (16.ix.1913, F.S.), bred from larva of fungus beetle, *Thallis janthina* (family Erotylidae).

Only the holotype is known. The black legs and antennae, striate mesopleuron, and complete absence of parapsidal furrows distinguish this species.

PROCTOTRUPES TURNERI Dodd

Proctotrupes turneri Dodd, 1920, Trans. Ent. Soc. Lond. 1919, 1920: 363.

Female

Shining black, antenna all dark; legs all reddish, except coxae; venation blackish; tegula reddish.

Head with scattered minute punctures and pubescence, transverse; eyes large and nearly bare; antenna long, filiform, segments longer than wide, apical club segment twice as long as wide; propleuron smooth, with a few striae in centre; mesopleuron smooth; scutum rather densely pubescent, scutellum similar, depressed at base; parapsidal furrow distinct only anteriorly; propodeum divided into 2 parts, anterior portion long, finely rugose, with distinct median carina, forking and diverging behind, posterior portion shorter and coarsely rugose; forewings long, broad, hyaline, pterostigma rather longer than wide, radial cell distinct but narrow, radial vein longer than the pterostigma; petiole not visible above; abdomen slightly convex above from lateral aspect, with a median sulcus and several short, lateral striae at base, otherwise smooth.

Male.—Femora dusky, otherwise as female.

Types.—Holotype and cotypes in the British Museum.

Type locality.—Mt. Wellington, Tas. (R. E. Turner).

There is a female from Lucindale, S.A. (A. M. Lea) in the South Australian Museum determined by Dodd. This agrees with the description of the type female except that only the hind coxae are dark.

The pale legs and smooth mesopleuron distinguish this species.

PROCTOTRUPES NITENS Dodd

Proctotrupes nitens Dodd, 1920, Trans. Ent. Soc. Lond. 1919, 1920: 364.

As specimens were not seen the description is taken from Dodd (1920).

Female

Shining black; legs fuscous, tarsi, bases and apices of femora and tibiae, yellow; antenna with scape yellow, otherwise black.

Head normal, vertex rather narrow, smooth and shining but with microscopic punctures, a distinct silvery pubescence below antennal insertions; scape stout, about as long as 1st funicle; pedicel very short; flagellum filiform, the segments slender, the 1st about 4 times, the penultimate about twice as long as wide; propleuron smooth, with several striae in the centre; mesopleuron entirely striate; metapleuron smooth for basal half, the remainder finely rugose; scutum smooth and shining, without distinct pubescence, wholly gently convex; scutellum convex, depressed at base; propodeum gradually declivous, not divided, finely rugose and with a deep, median longitudinal groove; forewing long, broad, hyaline but with a deep smoky patch beneath the pterostigma, venation fuscous, pterostigma large, as wide as long, the radial vein almost confluent with its distal margin, the radial cell thus subobsolete; basal, median, and recurrent veins faintly indicated; petiole not visible; base of abdomen without depression or striae; abdomen compressed, with a long compressed ovipositor, somewhat longer than the abdomen itself.

Male

Antenna wholly black, the segments hardly as long as in the female; smoky patch below the pterostigma small; base of propodeum smooth on either side of the median channel.

Types.—Holotype and allotype in the British Museum.

Type locality.—Yallingup, W.A. (Nov. 1913, R. E. Turner).

The yellow scape in the female, the fuscous legs marked with yellow, and the entirely striate mesopleuron distinguish this species.

PROCTOTRUPES DODDI, sp. nov.

Plate 1, Fig. 6

Female

Black; legs pale except coxae, trochanters, bases of femora narrowly, and less so tarsi; antennae brown-black; tegula pale.

Head, scutum, and scutellum smooth, with scattered, fine pubescence; eye nearly bare; propleuron smooth in part but with a horizontal series of several (9-10) striae increasing in length ventrad, the lower striae almost joining a series of foveae before the caudal margin on its lower half; mesopleuron smooth but with scattered hairs anterodorsally and ventrally; parapsidal furrows distinct only anteriorly; scutellum with a deep, undivided pit anteriorly; propodeum indistinctly divided into anterior and posterior portions, transverse carina indistinct but ornamentaton quite different, anteriorly with median and lateral carinae, the area between smooth anteriorly but becoming increasingly rugose posteriorly, posterior region rather abruptly declivous and then tapering caudally, strongly irregularly rugose, except caudally and there longitudinally striate; petiole not visible from above; abdomen only gradually convex above from its base (in lateral view), produced into a long ovipositor but only half as long as the rest of the abdomen; abdomen at base with a short median sulcus and lateral striae of two types, 2 or 3 short stout striae from base and several very fine sulci rather than striae extending almost in line with the caudal end of the median sulcus; forewing long, broad, hyaline but densely setose; venation fuscous; pterostigma only about as long as wide; radial vein longer than pterostigma, radial cell distinct; scape short and stout, not as long as 1st funicle, pedicel almost quadrate, 1st funicle at least 3 times as long as wide, succeeding shortening, penultimate almost twice as long as wide, apical segment longer, not quite as long as 1st funicle. Length, excluding ovipositor 4.5 mm; ovipositor 1.2 mm.

Type.—Holotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Barrington Tops, N.S.W. (5.ii.1931, A. P. Dodd).

The species differs from *nitens* in lacking ornamentation of the mesopleuron and from *turneri* in the structure of the propleuron. The species *janthinae* is quite distinct, lacking any sign of parapsidal furrows. It also has an ornamented mesopleuron. Only the holotype is known.

PROCTOTRUPES SPLENDIDUS, sp. nov.

Plate 1, Fig. 4

Female

Shining black; antenna all black; legs all reddish, except coxae and less so trochanters; venation fuscous; tegula reddish.

Head with scattered fine punctures and setae, transverse; eyes large, distinctly pubescent; face transversely rugose above the clypeus; antenna long, filiform, scape very short and stout, at most only twice as long as wide, pedicel transverse, funicle segments very long, 1st funicle at least 4 times as long as wide, 10th funicle at least 2½ times as long as wide; apical segment not as long as 1st funicle; propleuron mostly smooth, with 4 short, stout, longitudinal sulci at about the middle; mesopleuron mostly smooth, setae anterodorsally and ventrally, the normal row of foveae at the caudal margin and several distinct striae below towards the caudal margin; scutum and scutellum rather densely pubescent, scutellum depressed at base; propodeum not distinctly divided into 2 parts, with a distinct, strong, median longitudinal carina extending three-quarters of the way to the caudal margin, bordered on each side by a series of foveae which become elongated into irregular rugae caudad, lateral carina distinct only to level of spiracle, area mesad to this carina almost smooth, laterally propodeum coarsely rugose, short caudal region finely rugose and densely finely setose, propodeum without marked declivity; petiole very short; abdomen slightly convex above from lateral aspect, with a median sulcus at base, otherwise smooth at base except for the lateral rounded carina and tuft of hairs; forewing long, broad, hyaline but densely setose, pterostigma a little longer than wide, radial cell distinct, radial vein longer than pterostigma. Length, excluding ovipositor, 12.0 mm; ovipositor 3.5 mm.

Type.—Holotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Bendora, A.C.T. (21.iii.1951, E. F. Riek).

The species is most closely allied to *turneri* but differs in the structure of the propodeum and the eyes are distinctly hairy. Only the holotype is known.

Genus PHAENOSERPHUS Kieffer

Phaenoserphus Kieffer, 1908, in André, Spec. Hym. Eur. Alg. 10: 298.

Genotype *Proctotrupes curtipennis* Haliday, 1839, Hym. Brit. 1: 12 (designated by Muesebeck, Krombein, Townes, etc. 1951).

PHAENOSERPHUS AUSTRALIAE (Kieffer)

Proctotrypes australiae Kieffer, 1907, Berl. Ent. Z. 52: 266.
Phaenoserphus australiae Kieffer, 1914, Das Tierreich 42: 35.
Proctotrypes australiae Dodd, 1915, Trans. Roy. Soc. S. Aust. 39: 387.

Type locality.—Guildford, W.A.

The species has not been recognized.

Genus CRYPTOSERPHUS Kieffer

Cryptoserphus Kieffer, 1907, in André, Spec. Hym. Eur. Alg. 10: 288.

Genotype *Cryptoserphus longicalcar* Kieffer, 1908, in André, Spec. Hym. Eur. Alg. 10: 317 (designated by Kieffer, 1914).

CRYPTOSERPHUS NIGRISCUTUM Dodd

Cryptoserphus nigriscutum Dodd, 1915, Trans. Roy. Soc. S. Aust. 39: 388.

Female

Black; thorax red-brown, scutum somewhat darker, less so parapside and propodeum; tegula pale; legs all pale, golden yellow; antenna brown, scape yellow.

Head very transverse, with scattered short pubescence; scutum convex, smooth and with denser short pubescence, parapsidal furrows distinct only anteriorly; scutellum rather small, somewhat convex; propodeum divided into 2 portions, anterior part with a median and lateral carinae, the area between smooth, separated from the posterior portion by a transverse carina, posterior portion somewhat declivous, rugose, covered with dense whitish pubescence; petiole only narrowly visible from above; abdomen compressed, oval, with a filiform ovipositor nearly as long as the rest of the abdomen; abdomen at base with a fine median longitudinal sulcus and a few short, obscure carinae, its anterior margin carinate; forewing long, broad, subhyaline; pterostigma longer than greatest width, the radial vein longer than pterostigma; radial cell narrow; scape stout, somewhat shorter than 1st funicle, pedicel stout, quadrate, funicle segments slender, 1st much narrowed at base, the succeeding less so, 1st more than twice length of pedicel, succeeding shortening, penultimate 1⅓ times as long as wide, apical segment as long as 1st funicle.

Type.—Holotype ♀ in the South Australian Museum, Adelaide. Female on a card, antennae and forewings on a slide.

Type locality.—Cairns district, Qld. (18.ix.1913, A. P. Dodd), 1500 ft, sweeping.

One female, Macpherson Range, Qld., 2600 ft (Dec. 1929, A. P. Dodd) in the Division of Entomology Museum, C.S.I.R.O., Canberra, agrees with the above but the scape is only slightly pale below and the propleuron has a single short longitudinal sulcus at about its middle.

In 1 ♀ from Belgrave, Vic. (26.xii.1926, A. P. Dodd) in the Division of Entomology Museum, C.S.I.R.O., Canberra, the scape is pale at basal half, there are three short sulci on the propleuron, and the mesopleuron has a few weak striae below at caudal margin in addition to the normal marginal foveae.

CRYPTOSERPHUS NITIDUS Dodd

Plate 1, Fig. 5

Cryptoserphus nitidus Dodd, 1915, Trans. Roy. Soc. S. Aust. 39: 388.

Male

Shining black; legs, including coxae, tegula, scape, and pedicel, golden yellow.

Prothorax and mesothorax finely densely pubescent; parapsidal furrows present anteriorly; propodeum, petiole, and base of abdomen as in *nigriscutum;* forewing long, broad, hyaline; pterostigma somewhat longer than greatest width, the radial vein almost parallel with its distal margin; radial cell narrow; venation fuscous; 1st funicle segment 2½ times as long as wide, distinctly longer than 2nd, the 10th (penultimate) 1½ times as long as wide, the apical as long as the 1st funicle.

Type.—Holotype ♂ in the South Australian Museum. Male on a card, head, antennae, and forewings on a slide.

Type locality.—Cairns district, Qld. (24.vii.1913, A. P. Dodd), sweeping.

1 ♂, Cairns district (Dec. 1925, A. P. Dodd), agrees with the above description but the basal funicle segments are yellow below and the propleuron has three short transverse sulci (two carinae) at the middle of its height and towards the anterior margin and the anterolateral margin of the declivity is emarginate. Also the mesopleuron below is almost without hairs and has a few weak striae caudally near the margin.

This species is most probably the male of *nigriscutum*, the fine differences in antennal structure and difference in colour being most probably sexual.

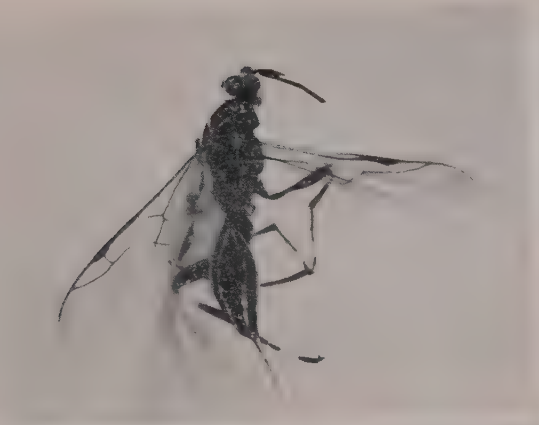
CRYPTOSERPHUS SULCATUS, sp. nov.

Female

Black with reddish hues, ovipositor not deep black; legs, including coxae, all pale, golden yellow; at least scape and pedicel golden yellow (remainder of antennae missing).

Ornamentation of head, scutum, and scutellum as in *nigriscutum;* propleuron with several (6-7) fine, short, somewhat radiating sulci situated in the middle towards the anterior margin; mesopleuron with a few weak striae below caudally; propodeum with median and lateral carinae over anterior half, the area between not smooth, but with irregular rugae becoming fainter and more longitudinally disposed anteriorly; a transverse carina at middle, posterior portion as in *nigriscutum;* abdomen at base with distinct median sulcus and on each side with several fine

AUSTRALIAN WASPS, FAMILY PROCTOTRUPIDAE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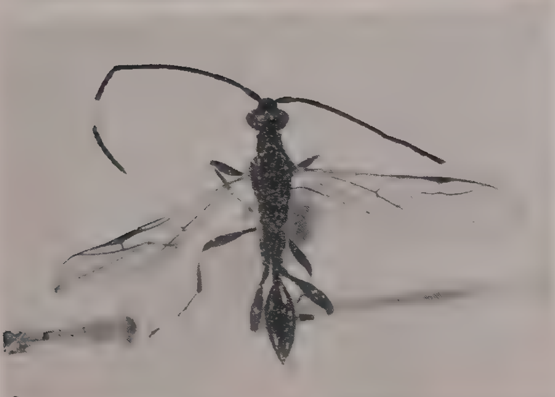
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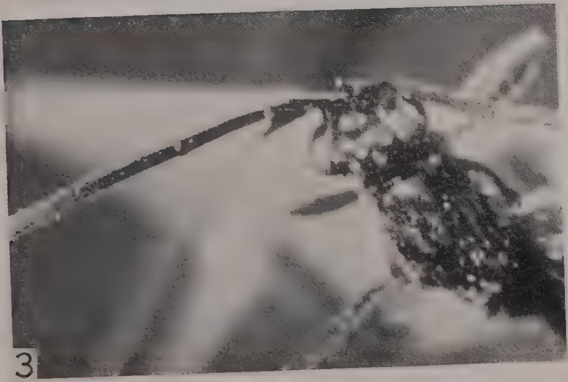
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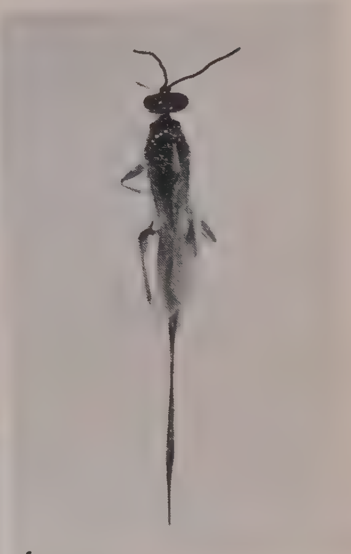
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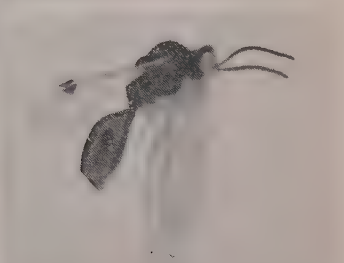
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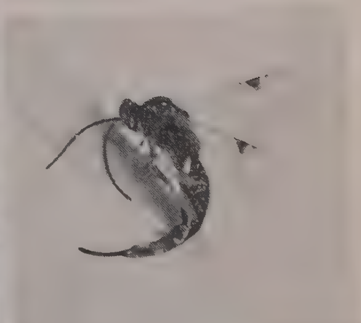
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striae converging towards the median sulcus. Length, excluding ovipositor, 3.0 mm; ovipositor 0.5 mm.

Type.—Holotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Marysville, Vic. (28.ii.1932, A. P. Dodd).

This species, though coming close to *nigriscutum*, can be distinguished on the ornamentation of the propleuron, propodeum, and base of the abdomen. Only the holotype is known.

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EXPLANATION OF PLATE 1

Fig. 1.—*Austroserphus albofasciatus* Dodd, paratype female. × *c.* 6.
Fig. 2.—*Austroserphus albofasciatus* Dodd, paratype male. × *c.* 6.
Fig. 3.—Head and antenna of Figure 2, enlarged.
Fig. 4.—*Proctotrupes splendidus*, sp. nov., holotype female. × *c.* 6.
Fig. 5.—*Cryptoserphus nitidus* Dodd, male, Cairns district. × *c.* 6.
Fig. 6.—*Proctotrupes doddi*, sp. nov., holotype female. × *c.* 6.

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AUSTRALIAN CLEPTID (HYMENOPTERA: CHRYSIDOIDEA) EGG PARASITES OF CRESMODODEA (PHASMODEA)

By E. F. Riek*

(*Manuscript received June 23, 1954*)

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Summary

Thirteen Australian species of this family are recorded. The nine new species described are placed in three new genera. Of the four species described by Kieffer two are retained in *Promesitius* and the other two, along with three of the new species, are placed in a separate new genus.

Introduction

In the course of research on the biology of the eucalypt-feeding phasmid, *Podacanthus wilkinsoni* Macleay, by the Division of Wood Technology, Forestry Commission of New South Wales, four species of hymenopterous parasites were bred from the eggs. These species are rather similar to *Promesitius coeruleus* Kieffer but divide naturally into two genera.

In addition to this bred material there are several other Australian species of which the host relationships are not known. All the known Australian material of this family is considered in this paper.

Kieffer (1905, 1907, 1914) described four species in the genus *Promesitius* Kieffer 1905. Only the female was known in all species. He placed the genus, with some doubt, in the Bethylidae, remarking that it showed affinity to the Chrysididae and less so to the Mutillidae.

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Now that winged males are known, at least some of the species placed in this genus by Kieffer are considered to belong to the Cleptidae.

It is considered that Kieffer's four species should be placed in two genera, but before discussing the matter an abridged key to Kieffer's species is given.

KEY TO KIEFFER'S SPECIES OF THE GENUS PROMESITIUS (AFTER KIEFFER)

1. At least pronotum yellow, head and abdomen dark; divisions of thorax not clearly defined..........2
   Head and at least dorsal side of thorax metallic blue; divisions of thorax clearly defined by sutures..........3
2. Thorax black with yellow pronotum; abdominal tergites finely, closely punctate *flavicollis*
   Thorax orange-yellow with 2 dark spots; abdominal tergites smooth, with scattered punctures..........*bimaculatus*
3. Abdominal tergites closely, finely punctate..........*coeruleus*
   Third tergite closely longitudinally lined, except on the lateral margins...... *punctaticeps*

In *flavicollis* and *bimaculatus* the divisions of the thorax are not clearly defined, while *coeruleus* and *punctaticeps* have the normal sutures. This character would seem to be sufficient to separate the two groups generically and as *flavicollis* is the type species of *Promesitius* a new generic name is required for *coeruleus* and *punctaticeps*.

Some doubt exists as to whether *Promesitius*, in this restricted sense, belongs to the Cleptidae. Of these four species only specimens of *coeruleus* were available for study so this matter cannot be settled definitely. *Promesitius* is dealt with in the family along with the new genus necessary for *coeruleus* and *punctaticeps* and others described below.

Family **CLEPTIDAE**

Only the typical genus *Cleptes* Latreille and a few other small genera have been placed in this family. The species of *Cleptes* are parasitic on sawfly larvae. Another genus often considered in the family, *Mesitiopterus* Ashmead, is a parasite of phasmid eggs.

Specimens of *Mesitiopterus* only were available for comparative study.

The Australian species, placed in three new genera described below, would appear to be more closely allied to *Cleptes* than is *Mesitiopterus*. As specimens of *Cleptes* were not available, comparison has been made with the Chrysididae.

All the Australian species have propodeal spines but *Mesitiopterus* lacks them. This latter genus is considered to show more affinity to the Bethylidae but differs in head shape, structure of mandibles and antenna, venation, and development of postscutellum. The Australian cleptids and *Mesitiopterus* form a connecting link between the Bethyloidea and Chrysidoidea, with *Mesitiopterus* more allied to the Bethylidae and the Australian cleptids to the Chrysididae.

The Australian species differ from the Chrysididae in several important characters. The females are wingless and structurally quite distinct from the males so only the latter are compared with the Chrysididae. They have the abdomen convex below and rounded at the base; propodeum with a transverse lamella at declivity; eyes hairy, pronotum long and face without a transverse carina above the scrobes. The Chrysididae, on the other hand, have the abdomen concave below and truncate at base, propodeum without a transverse lamella, eyes smooth, pronotum short, and the face usually with a transverse carina above the scrobes. The venation of the forewing differs, being more heavily sclerotized in the Chrysididae but with *M* ending well before the wing margin.

Mesitiopterus differs from the Australian cleptids mainly in the structure of the propodeum and development of the postscutellum. In *Mesitiopterus* the propodeum is without both the posterolateral spines and the transverse lamella at the declivity and the postscutellum is quite narrow at the meson.

Key to Australian Genera of the Family Cleptidae (including Promesitius)

Females

1. **Divisions of thorax not clearly defined**..........................*Promesitius*
   Divisions of thorax clearly defined by sutures..........................2

2. Declivity of propodeum glabrous; posterolateral spine of propodeum long, acute, as long as the 1st funicle segment; the pair of spines at declivity of propodeum long and acute, lamella not distinct; spines at apex of postscutellum well separated; 1st funicle less than half scape..........*Exova*, gen. nov.
   Declivity of propodeum transversely striate (at least in part); posterolateral spine of propodeum distinct but not as long as the 1st funicle segment; propodeum at declivity lamellate, at most with a pair of obtuse spines, lamella distinct; spines at apex of postscutellum almost touching; 1st funicle more than half scape..........................3

3. Abdominal tergites closely punctate (and setose); head above scrobes entirely punctate, punctures coarse and confluent, tending to be longitudinally lined; a distinct foveate zone laterally between postscutellum and propodeum..........*Ootheres*, gen. nov.
   Abdominal tergites glabrous, with scattered fine punctures (and setae); head above scrobes glabrous, with scattered punctures, sometimes close, but discrete; lateral region between postscutellum and propodeum mostly glabrous, wide..........................*Cresmophaga*, gen. nov.

Males

1. Punctures of abdomen not as dense on the 2nd segment as on the 3rd, setae very short so that the basal abdominal segments appear glabrous between the punctures..........................***Cresmophaga*, gen. nov.**
   Punctures of abdomen as dense on the 2nd segment as on the 3rd, setae dense, the whole surface of abdomen appearing finely setose..........*Ootheres*, gen. nov.

Genus PROMESITIUS Kieffer

Promesitius Kieffer, 1905, Ann. Soc. Sci. Bruxelles 29: 123.

Genotype *Promesitius flavicollis* Kieffer, 1905, loc. cit. 123 (original designation).

The divisions of the thorax are not clearly defined. In this character it is quite distinct from all other Australian genera and may not belong in this family. No specimens of the genus were available for examination.

PROMESITIUS FLAVICOLLIS Kieffer

Promesitius flavicollis Kieffer, 1905, Ann. Soc. Sci. Bruxelles 29: 123.
Promesitius flavicollis Kieffer, 1926, Das Tierreich 48: 291.

Type.—Female. Location not known.

Type locality.—Somerset, Australia.

PROMESITIUS BIMACULATUS Kieffer

Promesitius bimaculatus Kieffer, 1907, Berl. Ent. Z. 51: 291.
Promesitius bimaculatus Kieffer, 1926, Das Tierreich 48: 290.

Type.—Female. Location not known.

***Type locality.*—Mackay, Qld.**

Genus OOTHERES, gen. nov.

Genotype *Promesitius caeruleus* Kieffer, 1907, Berl. Ent. Z. 51: 290.

Female

Wings vestigial. Dorsal thorax with normal sutures; declivity of propodeum transversely striate; posterolateral spine of propodeum distinct but not as long as 1st funicle segment; propodeum at declivity lamellate, at meson with lamella emarginate; spines at apex of postscutellum almost touching; 1st funicle segment more than half as long as scape; abdominal tergites closely punctate (and striate); head above sockets entirely punctate, punctures coarse and confluent, tending to be longitudinally lined; ornamentation of dorsal thorax similar to that of head; mandible ending in a simple tooth; eyes hairy; tarsal claw with a tooth towards base.

Male

Fully winged. Structure quite distinct from that of female. Abdomen convex below, dorsally with the close punctures and setae of female; head similar but funicle segments after the 1st elongated, distinctly longer than wide; pronotum relatively shorter and scutum longer; parapsidal grooves percurrent, almost parallel; scutellum rather longer than in female; postscutellum rather shorter; declivity of propodeum with irregular rugae, not transversely striate; propodeal spines rather blunt; dorsal thorax and head closely punctate but punctures not tending to merge into longitudinal lines; wing venation as figured, Rs + M, M, and m − cu rather weaker than other veins; mandible bifid at apex; eyes strongly hairy; tarsal claw with a tooth towards base.

There is marked dimorphism in the sexes, possibly to some extent accentuated by the almost complete absence of wings in the female. Two of the five species included in the genus have been bred. Structurally the species are very similar. They differ mainly in the colour of body and legs. In most females there is an iridescent sheen on at least the dorsal thorax and head while in most males the body is black and lacks this sheen.

KEY TO SPECIES OF THE GENUS OOTHERES

*Females**

1. Dorsal thorax iridescent green-blue and purple. (Scape, pedicel, and basal funicle reddish)........*iridescens*, sp. nov.
Dorsal thorax iridescent blue-black........2
Dorsal thorax black. (Propodeum all red except narrowly at meson; antenna all dark)........*nigrithorax*, sp. nov.
2. Antenna all dark........*nigripedicel*, sp. nov.
Antenna red at scape, pedicel, and basal funicle........*coeruleus* (Kieffer)

Males

1. Dorsal thorax iridescent blue-green (lamella at propodeal declivity almost entire: tegula red-brown; legs dark; scape all dark).....*iridescens*, sp. nov.
Dorsal thorax black........2
2. Tegula red-brown (lamella at propodeal declivity distinctly emarginate; legs mostly dark; scape all dark)........*nigrithorax*, sp. nov.
Tegula black (lamella at propodeal declivity entire or nearly so)........3
3. Scape all black; legs all black or tibiae partly reddish but tarsi all dark.... *nigripedicel*, sp. nov.
Scape all black; legs black but all tibiae and metatarsi bright red........ *coeruleus* (Kieffer)

OOTHERES COERULEUS (Kieffer)

Plate 1, Fig. 3

Promesitius coeruleus Kieffer, 1907, Berlin. Ent. Z. 51: 290.
Promesitius coeruleus Kieffer, 1914, Das Tierreich 41: 291.

Female

Body dark above, lateral and ventral thorax and legs mostly red; antenna red at scape, pedicel, and basal funicle; propodeum red laterad of spine; legs with trochanters and less so coxae and femora partly dark, tarsi dark, less so middle tarsus; dorsal thorax iridescent blue-black, head less so, abdomen black.

Male

Body all black; legs black but all tibiae and metatarsi bright red; scape all dark; tegula black; lamella at declivity of propodeum entire or nearly so.

---

* The species *punctaticeps* (Kieffer) has been omitted as specimens were not examined.

Type.—Female. Location not known.

Type locality.—Mackay, Qld.

Specimens examined.—QUEENSLAND: Mackay (Jan. 1898), bearing also label R. E. Turner, 1910-225, 1 ♀; Brisbane (22.xi.1915, H. Hacker) 1 ♀. NEW SOUTH WALES: Jenolan Caves (29.vii.1952, M. Richards), emerged 20.xi.1952, bred from eggs of *Podacanthus wilkinsoni* Macleay, 1 ♂, 1 ♀.

The species is characterized in the female by the iridescent blue-black colouring of the dorsal thorax and the red scape, pedicel, and basal funicle segments. In the male the thorax is black, tegula black, scape black, and the tibiae and metatarsi are bright red.

The female from Jenolan Caves differs slightly from the topotypical specimen from Mackay and may possibly be distinct. The description of the male is based on the specimen from Jenolan Caves so, in the light of the variation shown by the female from this locality, it may not be typical.

OOTHERES PUNCTATICEPS (Kieffer)

Promesitius punctaticeps Kieffer, 1907, Berl. Ent. Z. 51: 291.
Promesitius punctaticeps Kieffer 1914, Das Tierreich 41: 291.

Type.—Female. Location not known.

Type locality.—Mackay, Qld.

Specimens of this species, which is characterized by the longitudinal lines on the third abdominal tergite, have not been examined.

OOTHERES IRIDESCENS, sp. nov.

Female

Body dark above, lateral and ventral thorax and legs mostly red; prothorax ventrally dark but not black; scape, pedicel, and basal funicle reddish; propodeum red laterally; legs with tarsi, trochanters, and fore femur partly dark; mandibles with dark transverse band in middle; dorsal thorax and head iridescent green-blue and purple, abdomen black.

Male

Dorsal thorax and head iridescent blue-green, dorsal abdomen less so and more blue, rest of body black; legs dark, lighter at joints and tarsi; scape all dark; tegula red-brown; lamella at propodeal declivity almost entire, with only a slight indentation narrowly at meson.

Types.—Holotype ♀, allotype ♂, and paratype ♂ and ♀♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra. Paratype, 1 ♀, in the U.S. National Museum.

Type locality.—Gogango, Qld.

Specimens examined.—QUEENSLAND: Gogango (Mar. 1928, Feb. 1930, 28.iii.1931, A. P. Dodd) 2 ♂♂, 5 ♀♀; Chinchilla (6.iii.1927, Jan. 1928, Feb. 1930, Feb. 1932, A. P. Dodd), 4 ♀♀.

The species is characterized by the iridescent blue-green hues of the dorsal thorax and head of both sexes though there is some purple in the female. The female has the base of the antenna reddish.

OOTHERES NIGRITHORAX, sp. nov.

Female

Body black above, without iridescent hues, lateral and ventral thorax and legs mostly red; antenna all dark but scape, pedicel, and basal funicle not black; propodeum all red except narrowly at meson; legs all red except for tarsi; dorsal thorax black.

Male

Body all black, but abdomen with reddish hues; legs all black or tibiae partly reddish but tarsi all darker; scape all dark; tegula red-brown; lamella at propodeal declivity emarginate.

Types.—Holotype ♀, allotype ♂, and 4 ♂♂ paratypes in the Division of Entomology Museum, C.S.I.R.O., Canberra. Paratype, 1 ♂, in the U.S. National Museum.

Type locality.—Pittwater, N.S.W.

Specimens examined.—NEW SOUTH WALES: Pittwater (16.iii.1930, 7.ii.1931, A. P. Dodd), 2 ♂♂, 1 ♀. QUEENSLAND: Tugun (26.iii.1932, A. P. Dodd) 1 ♂; Goondiwindi (Jan. 1928, A. P. Dodd), 2 ♂♂.

The species is characterized in the female by the black thorax. In all other species there is an iridescent sheen. The male has black thorax and red-brown tegula.

OOTHERES NIGRIPEDICEL, sp. nov.

Female

Body dark above; lateral and ventral thorax and legs partly red, prothorax ventrally mostly dark but not black; antenna all dark; propodeum red laterally; legs mostly red, tarsi dark, fore femur and hind tibia partly dark; mandibles red, with a dark transverse zone towards apex; dorsal thorax iridescent blue-black; head more black; abdomen black.

Male

Body all black, legs all black or tibiae partly, slightly reddish but tarsi all dark; scape all dark; tegula black; lamella at propodeal declivity entire or nearly so.

Types.—Holotype ♀, allotype ♂, and paratypes ♂♂ and 1 ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra. Paratypes in the Division of Wood Technology, Forestry Commission of N.S.W., Sydney.

Type locality.—Hassan's Walls, N.S.W.

Specimens examined.—NEW SOUTH WALES: Hassan's Walls (19.ix.1952, P. Hadlington), bred from eggs of *Podacanthus wilkinsoni* Macleay, emerged Dec. 1952, Jan. 1953, 6 ♂♂, 3 ♀♀.

The species is characterized in the male by being almost entirely black with only the joints and sometimes apices of tibiae lighter in colour. It has the black body colouring and black tegula of *coeruleus* but the tibiae and metatarsi are not clearly red. The female differs from *coeruleus* in having the antenna all dark.

Genus CRESMOPHAGA, gen. nov.

Genotype *Cresmophaga bispinosa,* sp. nov.

Female

Wings vestigial. Dorsal thorax with normal sutures; declivity of propodeum transversely striate (only partly so in *semiglabra,* sp. nov.); posterolateral spine of propodeum distinct but not as long as 1st funicle segment; propodeum at declivity lamellate, at most with a pair of obtuse spines but lamella still distinct; spines at apex of postscutellum almost touching; 1st funicle segment more than half as long as scape; abdominal tergites glabrous, with scattered fine punctures (and setae); head above scrobes glabrous, with scattered punctures, sometimes close, but discrete; ornamentation of dorsal thorax variable but usually with separate punctures; mandible ending in a simple tooth; eyes finely hairy; tarsal claw with a tooth towards base.

Male

Very similar to that of *Ootheres* but punctures of abdomen not as dense on the 2nd segment as on the 3rd and the setae of the abdomen finer.

The genus is distinguished on the structure of the propodeum and ornamentation of the abdomen. There are five species, which differ in ornamentation of the dorsal thorax and head. Three of them have been bred but the other two are without any host association.

KEY TO SPECIES OF THE GENUS CRESMOPHAGA

Females

1. Pronotum with punctures coarse and confluent, tending to be longitudinally lined. (Dorsal thorax black; head above scrobes with coarse punctures but glabrous between punctures; lamella at propodeal declivity truncate, slightly emarginate) .... *rugosinota,* sp. nov.
   Pronotum with scattered punctures, the space between glabrous............2
2. Lamella at propodeal declivity distinctly bifid, the teeth widely separated; head above scrobes coarsely punctate with small glabrous areas between the punctures (scutum with punctures tending to be confluent; antenna pale only at basal funicle)........................... *bispinosa,* sp. nov.
   Lamella at propodeal declivity almost entire; head above scrobes glabrous, with scattered fine punctures (antenna red at scape, pedicel, and basal funicle)..3
3. Scutum at caudal half longitudinally striate, scutellum similar except at meson; lateral ocelli almost touching eye; dorsal thorax all black.......... *striata,* sp. nov.

Scutum at caudal half with only the partially developed parapsidal grooves, scutellum without striae; lateral ocelli about their diameter from the eye; pronotum and propodeum mostly red.................*semiglabra*, sp. nov.

Males

1. Scape red below; femora and tibiae bright red or at most hind tibia partly darkened....................................*rubrifemur*, sp. nov.
   Scape all black or faintly reddish at base; legs all black or tibiae partly reddish 2
2. Punctures at ocelli coarser than those at vertex of head, all rather coarse.... *bispinosa*, sp. nov.
   Punctures at ocelli and at vertex of head similar, all rather fine........... *semiglabra*, sp. nov.

CRESMOPHAGA BISPINOSA, sp. nov.

Plate 1, Figs. 1 and 4

Female

Body shining black, thorax marked with red, legs mostly red; pronotum above variable, from all red to all black; postscutellum black at apex or all black; propodeum red except at meson; legs with femora and tibiae mostly red, otherwise mostly black; antenna at 1st funicle segment pale, with white setae; scape and pedicel sometimes pale below; mandible dark, a black cinctus in middle.

Dorsal thorax with scattered coarse punctures, closest on scutum and there tending to be confluent; lamella at declivity of propodeum distinctly bifid at meson, the teeth widely separated; head above scrobes coarsely punctate, with small glabrous areas between the punctures; lateral ocelli their diameter from the eye.

Male

Body all black; legs all black or tibiae partly reddish but tarsi all dark; scape all dark or narrowly reddish at base below; tegula black or darkened; lamella at propodeal declivity entire or nearly so; punctures at ocelli coarser than those at vertex of head, all rather coarse.

Types.—Holotype ♀, allotype ♂, and paratype ♂♂, ♀♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra. Paratype ♂♂, ♀♀ in the Division of Wood Technology, Forestry Commission of N.S.W., Sydney. Paratypes, 1 ♂, 1 ♀, in the U.S. National Museum.

Type locality.—Jenolan Caves, N.S.W.

Specimens examined.—NEW SOUTH WALES: Hassan's Walls (19.ix.1952, P. Hadlington), bred from eggs of *Podacanthus wilkinsoni* Macleay, emerged Dec. 1952, Jan. 1953, 8 ♀♀, 4 ♂♂; Jenolan Caves (11.viii.1953, M. Casimir) bred from eggs of *Didymuria violescens*, emerged Jan. 1954, 7 ♂♂, 5 ♀♀.

The species is characterized by the widely spaced teeth on the lamella at the propodeal declivity and the rather closely punctate head in the female and by the coarse punctures at the ocelli in the male.

CRESMOPHAGA RUGOSINOTA, sp. nov.

Female

Body black, thorax marked with red laterally and ventrally, legs mostly red; dorsal thorax all black; propodeum red only laterally; legs all red but coxae somewhat darkened; antennae missing; mandible red, with a black cinctus in middle.

Dorsal thorax with punctures coarse and confluent, tending to be longitudinally lined; lamella at declivity of propodeum truncate at meson, slightly emarginate; head above scrobes with coarse punctures but glabrous between punctures; lateral ocelli not quite their diameter from the eye.

Type.—Holotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Gogango, Qld.

Specimen examined.—QUEENSLAND: Gogango (Mar. 1928, A. P. Dodd), 1 ♀.

Only the holotype is known. The punctures of the pronotum are coarse and confluent, tending to be longitudinally lined. In all other species they are spaced.

CRESMOPHAGA STRIATA, sp. nov.

Plate 1, Fig. 5

Female

Body black, thorax marked with red, legs partly red; dorsal thorax black, except on lateral pronotum; propodeum red only laterally; legs all partly darkened, particularly femora and hind tibia; antenna red at scape, pedicel, and basal funicle; mandible red, with a wide, dark cinctus.

Dorsal thorax and head glabrous, with scattered, fine punctures; scutum, particularly at caudal half, longitudinally striate, the striae numerous, scutellum caudally striate except at meson; lamella at propodeal declivity almost entire; lateral ocelli almost touching the eye; postscutellum narrowly glabrous at meson and laterally.

Type.—Holotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Gogango, Qld.

Specimen examined.—QUEENSLAND: Gogango (Mar. 1928, A. P. Dodd), 1 ♀.

Only the holotype is known. It can be distinguished by the close longitudinal striae on the scutum and scutellum and also because the lateral ocelli are very close to the eye.

CRESMOPHAGA SEMIGLABRA, sp. nov.

Plate 1, Fig. 6

Female

Body black, thorax widely marked with red, legs partly red; pronotum variable, usually red but dark discally towards caudal margin; scutum usually all dark, sometimes red discally; postscutellum red, dark at apex; propodeum all red; legs all partly darkened, particularly hind legs; antenna red at scape, pedicel, and basal funicle; mandible red, with a dark cinctus.

Dorsal thorax and head glabrous with scattered fine punctures; scutum without striae, with only the partially developed parapsidal sutures; postscutellum widely glabrous laterally; lateral ocelli almost their diameter from the eye.

Male

Body all black; legs black but all tibiae partly reddish, less so femora; scape narrowly reddish at base below and mesally; tegula black or darkened; lamella at propodeal declivity entire or nearly so; punctures at ocelli similar to those at vertex, all rather fine.

Types.—Holotype ♀, allotype ♂, and paratype ♂♂, ♀♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra. Paratype ♂♂, ♀♀ in the Division of Wood Technology, Forestry Commission of N.S.W., Sydney. Paratypes, 1 ♂, 1 ♀, in the U.S. National Museum.

Type locality.—Jenolan Caves, N.S.W.

Specimens examined.—NEW SOUTH WALES: Hassan's Walls (19.ix.1952, P. Hadlington), bred from eggs of *Podacanthus wilkinsoni* Macleay, emerged Dec. 1952, Jan. 1953, 4 ♀♀, 3 ♂♂; Jenolan Caves (11.viii.1953, M. Casimir), bred from eggs of *Didymuria violescens*, emerged Jan. 1954, 2 ♀♀, 2 ♂♂.

The species has rather spaced punctures on all the dorsal thorax and head of the female, which distinguishes it from the other three species. The male has the punctures of the head uniform and the tibiae are always partly reddish.

CRESMOPHAGA RUBRIFEMUR, sp. nov.

Plate 1, Fig. 2

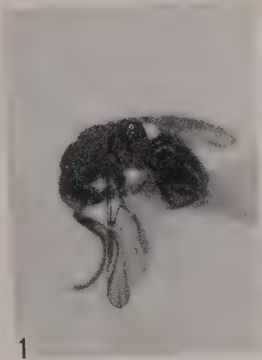
Male

Body all black; legs with all femora and tibiae bright red or hind tibia partly darkened, otherwise legs black or dark; scape red below; tegula black; lamella at propodeal declivity almost entire.

Types.—Holotype ♂ and paratype ♂ in the Division of Entomology Museum, C.S.I.R.O., Canberra. Paratype ♂ in the Division of Wood Technology, Forestry Commission of N.S.W., Sydney. Paratype, 1 ♂, in the U.S. National Museum.

Type locality.—Hassan's Walls, N.S.W.

AUSTRALIAN CLEPTID EGG PARASITES OF CRESMODODEA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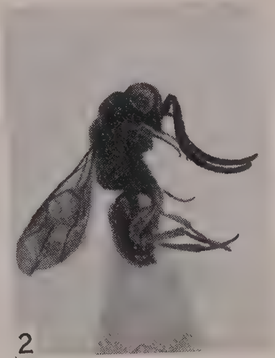
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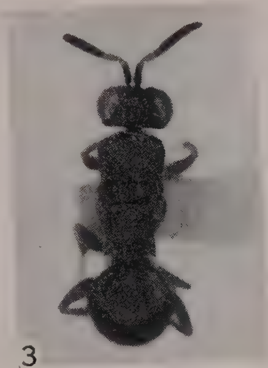
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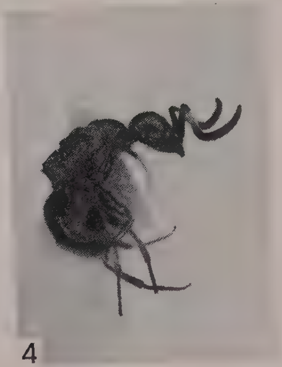
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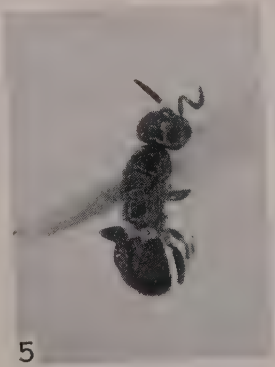
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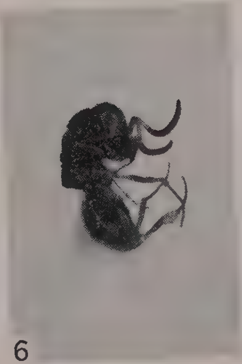
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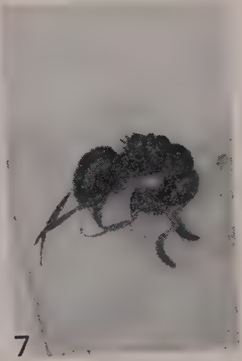
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Specimens examined.—NEW SOUTH WALES: Hassan's Walls (19.ix.1952, P. Hadlington), reared from eggs of *Podacanthus wilkinsoni* Macleay, emerged Dec. 1952, 3 ♂♂; Jenolan Caves (11.viii.1953, M. Casimir) bred from eggs of *Podacanthus wilkinsoni* Macleay, emerged Jan. 1954, 3 ♂♂.

Only the male is known. It has most distinctively coloured legs and scape.

Genus EXOVA, gen. nov.

Genotype *Exova tetraspina*, sp. nov.

Female

Dorsal thorax with normal sutures; declivity of propodeum glabrous; posterolateral spine of propodeum long, acute, as long as the first funicle segment; the pair of spines at declivity of propodeum long and acute, lamella not distinct; spines at apex of postscutellum well separated; 1st funicle less than half scape; abdominal tergites glabrous, with scattered fine punctures (and setae); head above scrobes glabrous, with scattered punctures, rather numerous; pronotum glabrous, with scattered punctures; mandible ending in a simple tooth; eyes hairy; tarsal claw with a tooth towards base.

The genus is characterized by the structure of the propodeum, postscutellum, and antenna. Only the one species is known.

EXOVA TETRASPINA, sp. nov.

Plate 1, Fig. 7

Female

Body black, lateral and ventral thorax mostly red, legs mostly red; dorsal thorax black, declivity of propodeum red; legs with femora and tibiae partly darkened, apices of coxae white; antenna red at scape, pedicel, and basal funicle; mandible red.

Head glabrous, with rather numerous punctures; pronotum glabrous, with rather widely spaced punctures; scutum over caudal half and postscutellum, irregularly, longitudinally lined, less so scutellum; punctures of abdomen very fine and widely spaced, the setae long; lateral ocelli almost touching the eye.

Types.—Holotype ♀ and paratype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Mt. Tambourine, Qld.

Specimens examined.—QUEENSLAND: Mt. Tambourine (6.iii.1927, A. P. Dodd), 2 ♀♀.

ACKNOWLEDGMENTS

I am most grateful to Mrs. J. Mary Casimir, of the Division of Wood Technology, for the opportunity to study the material bred by her from

phasmid eggs and the enthusiasm she has shown in obtaining additional material. Most of the non-bred material was collected by A. P. Dodd and recently presented by him, along with the remainder of his private collection of Proctotrupoidea and other parasitic Hymenoptera, to the Division of Entomology, C.S.I.R.O., Canberra. I very much appreciate his generosity and help in the study of parasitic Hymenoptera. The photographic illustrations of the plate were prepared by Mr. D. Wilson, Division of Entomology, C.S.I.R.O., Canberra.

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EXPLANATION OF PLATE 1

Fig. 1.—*Cresmophaga bispinosa*, gen. et sp. nov., allotype male. × *c.* 8.
Fig. 2.—*Cresmophaga rubrifemur*, gen. et sp. nov., holotype male. × *c.* 8.
Fig. 3.—*Ootheres coeruleus* (Kieffer), female from Brisbane. × *c.* 8.
Fig. 4.—*Cresmophaga bispinosa*, gen. et sp. nov., holotype female. × *c.* 8.
Fig. 5.—*Cresmophaga striata*, gen. et sp. nov., holotype female. × *c.* 8.
Fig. 6.—*Cresmophaga semiglabra*, gen. et sp. nov., paratype female. × *c.* 8.
Fig. 7.—*Exova tetraspina*, gen. et sp. nov., holotype female. × *c.* 8.

AUSTRALIAN AMPULICIDAE (HYMENOPTERA: SPHECOIDEA)

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Summary

The paper deals with the systematics of the Australian representatives of this small family of predatory wasps. Four new species of *Aphelotoma* are described and a new genus, *Austrotoma*, erected for *Aphelotoma aterrima* Turner. A single species only of *Dolichurus* is recorded. Ten Australian species and one subspecies are recognized in the paper.

INTRODUCTION

This small distinct family of the Sphecoidea contains few genera, the species of which, in all known cases, are predators of cockroaches. The species are widespread in Australia but, because of the habit of foraging for their prey in dead leaves and rubble and under bark, they are not commonly seen. Normally, males are collected when they alight on living tree trunks, and occasionally females are taken there too. A smooth-barked eucalypt in direct sunlight seems to be the preferred point of alighting for males. The females prefer dead trees and stumps. Specimens have been observed flying only in direct sunlight. When seen from a distance, their jerky walking action on tree trunks resembles that of ants of the genus *Myrmecia*. There is also a superficial resemblance to the ants in shape if one excludes the wings of the ampulicid.

The ampulicids have a very long prothorax, in which character they are approached by *Nitela* (Larridae) but they can be distinguished on wing venation. They are separated readily also on the middle tibial spurs. *Nitela*, though of smaller size, has the habit of alighting on tree trunks and running over the bark in a manner similar to that of the ampulicids. There is a superficial resemblance to some psammocharids which also have this habit of hunting under loose bark on trees, but in their case for spiders and not for cockroaches.

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Two genera of the family have been recognized in the Australian fauna and a third genus, originally described in this family, was later transferred to the Nitelidae (Larridae). Most of the species belong to the endemic genus *Aphelotoma* but one species of the widespread *Dolichurus* is also recorded. Most of the published work is contained in a series of papers by Turner (1907-1916) who gives partial keys to the species of *Aphelotoma*. Additional species of *Aphelotoma* are recorded in this paper and a new genus, *Austrotoma*, is erected for *Aphelotoma aterrima* Turner.

The main characters of the family are: Eyes large, reaching the base of the mandibles or nearly as far, their inner margins parallel or converging above; ocelli round and normal; maxillary palpi 6-, labial palpi 4-segmented; antenna 12-segmented in the female, 13-segmented in the male, the flagellum long and filiform; prothorax long, the collar well developed; propodeum quadrate, the dorsum with two or more distinct and oblique carinae or reticulate-rugose, the posterior lateral angles dentiform (except in *Aphelotoma*), or the lateral margins of the declivity dentate at about the middle; abdomen more or less petiolated (except in *Dolichurus* and *Austrotoma*), the petiole formed by the first free tergite and sternite; anterior wing with two or three cubital cells and two recurrent veins; middle tibia with two spurs; tarsal claws with one or two teeth.

KEY TO GENERA OF THE FAMILY AMPULICIDAE OCCURRING IN AUSTRALIA

1. Antennae inserted under a tegular protuberance. (Lateral margins of the propodeal declivity furnished with a triangular tooth near or below the middle; abdomen sessile; pronotum with anterolateral protuberances)...... *Dolichurus* Latreille

Antennae not inserted under a tegular protuberance.....................2

2. Lateral margins of the propodeal declivity furnished with an acute spine slightly above the middle; abdomen without distinct petiole; pronotum without anterolateral protuberances...............*Austrotoma*, gen. nov.

Lateral margins of the propodeal declivity without a spine; abdomen with a short petiole; pronotum with anterolateral protuberances............. *Aphelotoma* Westwood

Genus APHELOTOMA Westwood

Aphelotoma Westwood, 1842, Trans. Ent. Soc. Lond. 3: 225.

Genotype *Aphelotoma tasmanica* Westwood, 1842, loc. cit (original designation).

Mandible sickle-shaped with an acute apex; in the female clypeus clearly defined, with truncate apex; labrum distinct with more or less parallel sides and with truncate or slightly emarginate apex; antenna filiform, with funicle segments long, decreasing regularly in length; antennal sockets lying on the face, not covered by porrect lamella, insertions about as wide apart as each is from the eye; pronotum large, with, at least, distinct anterolateral protuberances; mesonotum divided longitudinally into 3 subequal areas by 2 deep sulci; lateral margin of propodeal declivity without spine or tubercle, a transverse carina at the junction of the dorsal portion and the declivity; abdomen with a small, distinct petiole formed from the tergite and sternite of the 1st free segment (segment 2 of abdomen); 4th tarsal segment not enlarged.

The coloration, particularly of legs and antennae, is very different in the sexes of some species. For example, in *tasmanica* the female has red legs and darkened antenna while the male has darkened legs and considerably more red in the antenna. The colour difference has rendered the association of the sexes rather difficult, particularly also as there are marked structural differences between the sexes. The position of the second recurrent vein was used as a character by Turner. It is very variable in the one species and may even occur before the second transverse cubital vein, though it is normally in line with it or occurs after it.

Key to Species of the Genus Aphelotoma

Males

1. Face with short hairs, less than half as long as scape; abdomen without dense pubescence, but with scattered setae on segments 4 and succeeding ones; face irregularly foveate........................2

Face with long hairs, more than half as long as scape; abdomen with dense pubescence at least after segment 3; face only with very fine pits forming fine irregular vertical rugae........................3

2. Abdomen above at least red in part. (Legs mostly red; antenna red at scape, pedicel, and 1st funicle segment; tegula black)..........*rufiventris* Turner

Abdomen above all black. (Antenna reddish at scape, pedicel, and basal funicle segment; tegula dark reddish; legs mainly red but all tarsi darkened and less so tibiae; at least fore coxa darkened or black; fore femur red or darkened)........................*melanogaster*, sp. nov.

3. Antenna red except for apical 4 or 5 segments; abdomen with pubescence not distinct laterally on segment 3. (Legs with apices of femora, all of tibiae, and tarsi red)........................4

Antenna all dark or with only scape, pedicel, and base of 1st funicle segment red; abdomen with pubescence distinct laterally on segment 3............5

4. Hind femur with at least the apical third red; pubescence silvery..........*tasmanica* Westwood

Hind femur with not more than the apical quarter red; pubescence with golden tinge........................*tasmanica auriventris* (Turner)

5. Antenna all dark, somewhat lighter at base; legs black, tibiae and tarsi lighter or red but hind femur always darkened........*nigricula*, sp. nov.

Antenna dark, distinctly red at scape, less so pedicel and base of 1st funicle segment; legs black in part, all tibiae and tarsi and hind femur red, middle femur variable........................*auricula*, sp. nov.

Females

The species *striaticollis* and *affinis* are not included in the key as the original descriptions are inadequate.

1. Median sulcus of pronotum bordered by a distinct carina, apex of labrum notched; antenna with scape, pedicel, and basal funicle segments red. (No obvious pubescence laterally on segment 3 of abdomen; legs red, darkened in part, particularly femora and tibiae) ....*melanogaster*, sp. nov.
   Median sulcus of pronotum not bordered by a carina; apex of labrum truncate; antenna with scape, pedicel, and most or all funicle segments dark 2
2. No obvious pubescence laterally on segment 3 of abdomen..................3
   Pubescence distinct laterally on segment 3 of abdomen.....................4
3. Legs red, joints narrowly and hind tarsus darkened, coxae and hind tibia variable; antenna red or reddish on funicle segments 3-4................ *tasmanica* Westwood
   Legs red, joints narrowly and all tarsi darkened, hind tibia slightly darkened; antenna all dark......................*tasmanica auriventris* (Turner)
4. Legs all black but under surface of tarsi lighter; body all black except for tarsi and apex of mandible; pubescence very distinct, golden............ *fuscata*, sp. nov.
   Legs black except for most of femora and coxae, tarsi all black; body all black except for legs and apex of mandible; pubescence golden.......... *nigricula*, sp. nov.

APHELOTOMA RUFIVENTRIS Turner

Plate 1, Fig. 1

Aphelotoma rufiventris Turner, 1914, Proc. Linn. Soc. N.S.W. 38: 619.

Male

Head and thorax black, abdomen red, sometimes with the apical segments darkened; antenna red at scape, pedicel, and base of 1st funicle; mandible red except for extreme base and apical tooth; tegula reddish, darkened; legs all red except darkened fore coxa, trochanter, and less so femur, darkening of trochanter and femur variable, sometimes all red.

Abdomen shining, segments 2 and 3 with scattered punctures, 4 and succeeding with denser punctures and scattered setae, more so laterally, segments not densely clothed in setae.

Small species, length 5 mm; pronotum with both anterolateral and posterodorsal projections prominent; face between ocelli and antennae irregularly foveate, not vertically lined; inner margins of the eyes almost straight, diverging ventrally; setae of the face short and pale, not half as long as the scape; femoral furrow of the fore legs with a few strong transverse rugae.

Female.—Unknown.

Type.—Holotype ♂ in the British Museum.

Type locality.—Kuranda, Qld. (May to July).

Locality records.—QUEENSLAND: Stradbroke I.; Stanthorpe (2.ii.1930); Caloundra (28.ix.1913); 10 miles S. of Bowen (27.ix.1950, E. F. Riek).

There is some variation in the colour of the abdomen but at least the basal half is red.

APHELOTOMA MELANOGASTER, sp. nov.

Plate 1, Figs. 2 and 3

Male

Abdomen all black; antenna red at scape, pedicel, and base of 1st funicle, sometimes 1st and base of 2nd; mandible red except at extreme base and at apical tooth; tegula reddish, darkened; legs mostly red, tibiae and tarsi darkened, particularly behind, fore femur darkened, less so middle and hind femora above, colouring of femora and fore tibia variable, sometimes all red.

Abdomen shining, segments 2 and 3 with scattered punctures, segment 4 and succeeding segments with denser punctures and scattered setae, more so laterally, segments not densely clothed in setae.

Small species, length 6 mm; pronotum with both anterolateral and posterodorsal projections prominent; face between ocelli and antennae irregularly foveate, tending to be vertically lined; setae of face short and pale, not half as long as scape; femoral furrow of the fore legs with a few strong transverse rugae.

Female

Body black; antenna red at scape, pedicel, and basal 4 funicle segments; mandible red except for extreme base and for apex of tooth; tegula blackish; legs darkened red to reddish black, more so the coxae and fore femur.

Abdomen shining, segments 2 and 3 glabrous with a few scattered fine punctures with setae, more so laterally on segment 3; segment 4 and succeeding segments densely clothed in short, white setae.

Small species, length 6.5 mm; face with a small median projection somewhat above the level of the antennae; pronotum with an open median sulcus bordered on each side by a low, rounded carina, the 2 carinae suddenly meeting anteriorly and becoming indistinct posteriorly, faint irregular rugae between this area and the distinct dorsolateral carina; labrum with apex distinctly notched, sides converging slightly; clypeus with only long, scattered setae; lower half of the face with distinct, white setae.

Types.—Holotype ♂, allotype ♀, and paratype ♂♂ and ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Blundells, A.C.T. (15.iii.1950, E. F. Riek).

Locality records.—A.C.T.: Blundells (13.ii.1950, E. F. Riek); Tharwa (14.ii.1951, E. F. Riek); Black Mt., Canberra (17.ii.1930, 5.iv.1930, L. F. Graham). NEW SOUTH WALES: Western slopes of Barrington Tops, (11.iv.1949, E. F. Riek). QUEENSLAND: Brisbane (Jan. 1924, H. Hacker).

This species differs from *rufiventris*, in the male, principally in colour and can be separated at once on the abdomen being entirely black and the tarsi darkened. In one specimen from Barrington Tops segments 2 and 3 of the abdomen have a reddish hue.

APHELOTOMA TASMANICA Westwood

Plate 1, Figs. 4, 5, 13, and 14

Aphelotoma tasmanica Westwood, 1842, Trans. Ent. Soc. Lond. 3: 225.
Aphelotoma tasmanica Turner, 1915, Ann. Mag. Nat. Hist. (8) 15: 64.

Male

Body black; antenna red except for the apical 4 or 5 segments; mandible red except for base and for the apical tooth; tegula black; legs black at base, tarsi, tibiae, and apices of femora red, at least apical third of hind femur red, sometimes nearly all red.

Abdomen shining at base, segments 2 and 3 with scattered punctures, segment 3 laterally with very fine, but not conspicuous setae, segment 4 and succeeding segments silvery, clothed in dense fine setae with a few longer setae laterally.

Larger species, length 7 mm but occasionally as small as 5.5 mm; pronotum with the anterolateral projections small so that the lateral margin bulges in the middle; face between the ocelli and antennae with fine pits forming irregular vertical rugae, appearing relatively smooth as compared with *rufiventris;* inner margins of the eyes concave with the lower halves almost parallel; setae of face very long and conspicuous, almost as long as the scape; scape with long setae on the inner margin; femoral furrow of the forelegs with fine irregular rugae anteriorly, glabrous in part behind.

Female

Body black; antenna black but reddish at the 3rd and 4th funicle segments, scape dark reddish; mandible black except a small area at the bases of the teeth; tegula black; legs mostly red, hind tarsus and apical segment of fore and middle tarsi dark, tibiae variable, particularly the hind tibia, which may be black.

Abdomen shining at base, segments 2 and 3 glabrous with very few, scattered, fine punctures and setae, more so laterally on segment 3; segment 4 and succeeding segments densely clothed in short, white setae.

Large species, length 10-11 mm; face without a median projection, tending to be finely vertically lined, pronotum with a shallow, open, median sulcus not bordered by distinct carinae and dorsolateral carina rounded;

labrum tapering slightly to the transverse apex; clypeus densely setose; lower half of face with distinct white setae.

Type.—Holotype ♀. Location not known.

Type locality.—Tasmania.

Locality records.—TASMANIA: Hobart (4.i.1951, E. F. Riek); Southport (18.i.1948, E. F. Riek); 8 miles E. of Scottsdale (9.i.1949, E. F. Riek); Triabunna (24.xii.1915, G. H. Hardy); Launceston (7.i.1917, G. H. Hardy).

There are marked colour differences between the sexes, the female having dark antenna and red legs, the male red antenna and darkened legs.

Turner examined only females from Tasmania and associated males from Victoria with them. These males most probably belong to the subspecies *auriventris.*

APHELOTOMA TASMANICA AURIVENTRIS (Turner)

Plate 1, Fig. 6

Aphelotoma auriventris Turner, 1907, Ann. Mag. Nat. Hist. (7) 19: 269.
Aphelotoma auriventris Turner, 1910, Proc. Zool. Soc. Lond. 1910: 341.

Male

Differs from the typical subspecies in the colour of the legs and the pubescence of the abdomen. Legs with tibiae and tarsi and only the extreme apices of the femora red, hind femur with not more than the apical one-quarter red.

Ornamentation of the abdomen normal but the pubescence with a distinct golden tinge and rather long.

Pronotum with both the anterolateral and posterodorsal projections small and rather rounded.

Female

Body black; antenna appearing all dark with slightly lighter scape; mandible black, red at base of teeth; tegula black; legs red, with black tarsi and narrowly black at joints.

Abdomen shining at base, segment 2 glabrous, with only very few, scattered, fine punctures and setae, segment 3 similar at meson, lateral half with numerous fine punctures and setae, segment 4 and succeeding segments densely clothed in rather long, golden setae.

Type.—Holotype ♂ in the British Museum.

Type locality.—Victoria.

Locality records.—A.C.T.: Mt. Franklin (24.i.1950, E. F. Riek); Bendora (24.i.1950, 2.iii.1949, E. F. Riek); Blundells (24.iii.1949, E. F. Riek). Turner (1915) recorded this species from Grampian Hills, Vic.; Kangaroo I., S.A., and Yallingup, south-west Australia.

Turner's original description is that of a male, not female as stated by him. The male recorded in 1910 would appear to be a darker variant or possibly the species *nigricula.*

APHELOTOMA NIGRICULA, sp. nov.

Plate 1, Fig. 10

Male

Body black; antenna all dark, sometimes lighter or reddish at scape, pedicel, and basal funicle segments; mandible black, reddish in the middle; tegula black; legs black, lighter and sometimes reddish over the tibiae and tarsi.

Abdomen shining at base, segment 2 with rather dense punctures, segment 3 with punctures more scattered at meson, those laterad and at posterior margin small and dense, laterally with conspicuous, fine, dense, golden setae, segment 4 and succeeding segments completely covered with conspicuous, dense, golden pubescence.

Specimens from Blundells, the type locality, show the colour variations mentioned above. Some colouring of the tibiae, tarsi, and antennae seems to be more typical.

Larger species, length 6-7 mm; pronotum with anterolateral projections reduced; face between ocelli and antennae with fine pits forming irregular vertical rugae; inner margins of the eyes concave, their lower halves almost parallel; setae of face long and conspicuous, more than half as long as the scape; femoral furrow of forelegs with fine irregular rugae anteriorly, glabrous in part behind.

Female

Body black; antenna all dark, with a slightly lighter scape; mandible black, red at base of teeth; tegula black; legs partly red, all tarsi black, all tibiae mostly black, all femora narrowly black at apex, all trochanters and fore coxa partly darkened, posteromesal surface of hind femur black.

Abdomen shining at base, segment 2 glabrous, with only very few, scattered, fine punctures and setae, segment 3 similar at meson, lateral half with numerous fine punctures and golden setae, segment 4 and succeeding segments densely clothed in rather long, golden setae.

Large species, length 10 mm; face with a small median projection above the level of the antennae and a faint carina below the median ocellus, face vertically lined; pronotum with a rather deep, sharply margined, median sulcus, dorsolateral carina rounded, the space between with irregular elongated pits; the labrum with sides converging slightly to the transverse apex; clypeus densely setose; lower half of face with distinct white setae.

Types.—Holotype ♂, allotype ♀, and paratype ♀, ♂♂ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Blundells, A.C.T. (15.iii.1950, E. F. Riek); allotype, 9 miles W. of Goulburn, N.S.W. (13.ii.1953, E. F. Riek).

Locality records.—A.C.T.: Blundells (9.ii.1949, E. F. Riek); Spring Range, Canberra (3.ii.1929, M. Fuller). NEW SOUTH WALES: Western slopes of Barrington Tops (11.iv.1949, E. F. Riek); 9 miles W. of Goulburn (13.ii.1953, E. F. Riek); 20 miles E. of Canberra (20.xi.1953, E. F. Riek). QUEENSLAND: Stanthorpe (7.ii.1930).

Structurally the species seems to differ from *tasmanica* only in the ornamentation of segments 2 and 3 of the abdomen.

APHELOTOMA AURICULA, sp. nov.

Plate 1, Fig. 8

Male

Body black; antenna black, distinctly red at scape, pedicel, and base of 1st funicle; mandible red, black widely at base and at apical tooth; tegula black; legs red except coxae, trochanters, and fore femur, middle femur variable, sometimes darkened.

Abdomen shining at base, segment 2 with rather dense punctures but narrowly glabrous at meson, segment 3 with similar glabrous area at meson, punctures laterad rather small and dense, with conspicuous, rather long, dense, deep golden pubescence laterally, narrowly at anterior margin and widely at posterior margin, segment 4 and succeeding segments completely covered with similar pubescence.

Larger species, length 7 mm; pronotum with anterolateral and particularly posterodorsal projections; face between ocelli and antennae with fine pits forming irregular vertical rugae; inner margins of the eyes concave, lower halves almost parallel; setae of face long and conspicuous, almost as long as scape; femoral furrow of fore legs with fine irregular rugae anteriorly, glabrous in part behind.

Types.—Holotype ♂ and paratype ♂♂ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Ten miles S. of Bowen, Qld. (27.ix.1950, E. F. Riek).

Locality record.—QUEENSLAND: Caloundra (28.ix.1913).

The species is characterized by the abundant, deep golden pubescence of the abdomen. It differs from *nigricula* slightly in ornamentation of the abdomen and in the colour of the legs and antennae. This may possibly be the male of *striaticollis* described from a female collected at Townsville, Qld.

APHELOTOMA FUSCATA, sp. nov.

Plate 1, Fig. 7

Female

Body black; antenna black, the apical segments with a slight reddish hue; mandible black, red at the bases of the teeth; tegula black; legs black, tarsi somewhat lighter ventrally.

Abdomen shining at base, segment 2 glabrous, with a few, small scattered punctures and setae, segment 3 similar at meson, each lateral third of the segment and anterior and posterior margins finely, closely punctate and setose, setae long at the lateral margin, segment 4 and succeeding segments clothed in a long, dense, golden pubescence.

Large species, length 11 mm; face with a small median projection just above the level of the antennae and a faint carina below the median ocellus, face vertically lined; pronotum with a rather deep, sharply margined, median sulcus, dorsolateral carina rounded, the space between with irregular elongated pits; the labrum with sides converging slightly to the transverse apex; clypeus densely setose; lower half of face with distinct white setae.

Type.—Holotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Catherine Hill, N.S.W. (12.iv.1949, E. F. Riek).

This is a large black species with very obvious golden pubescence on the abdomen. Only the holotype is known.

APHELOTOMA STRIATICOLLIS Turner

Aphelotoma striaticollis Turner, 1910, Proc. Zool. Soc. Lond. 1910: 341.

This species has not been recognized so Turner's original description is given.

"♀. Clypeus small, shining; the labrum prominent and notched at the apex. Mandibles very sharply bent near the base, the apical half falcate and acute at the apex, the basal half much broadened, with a tooth near the middle of the inner margin. Antennae inserted much further from each other than from the eyes, filiform; the second joint of the flagellum as long as the first joint and the scape combined. Head opaque, the front very finely and indistinctly longitudinally striated, the inner margin of the eyes nearly parallel; the posterior ocelli nearer to the eyes than to each other. Pronotum much narrower than the head, longer than the mesonotum, longer than broad, finely rugose, the sides raised and forming marginal carinae, two parallel longitudinal carinae close together near the middle reaching from the anterior to the posterior margin. Mesonotum and scutellum coarsely longitudinally rugose; propleurae finely, mesopleurae coarsely rugose. Median segment very coarsely reticulate, the sides obliquely striated, vertically truncate posteriorly, longer than the pronotum, broader than long. Abdomen smooth and shining, the third and following segments very minutely punctured. First recurrent nervure received beyond two-thirds from the base of the first cubital cell, second received near one-fifth from the base of the third cubital cell. The branch nervure from the first transverse cubital nervure reaching into the first cubital cell is very short. Black; the mandibles and the apical joints of the tarsi beneath fusco-ferruginous; abdomen shining bronze. Wings fusco-hyaline, clearer at the apex, with a broad hyaline band crossing the first cubital cell; nervures fuscous, testaceous in the hyaline band.

Length 8 mm.

Hab. Townsville, Q. (F. P. Dodd October)" (Turner).

On the structure of the labrum, position of ocelli, and the presence of a pair of median carinae on the prothorax this species appears to be allied to *rufiventris* and *melanogaster* but it has the obvious abdominal pubescence of the other species. Its small size is more in keeping with the first group.

APHELOTOMA AFFINIS Turner

Aphelotoma affinis Turner, 1910, Proc. Zool. Soc. Lond. 1910: 341.
Aphelotoma affinis Turner, 1915, Ann. Mag. Nat. Hist. (8) 15: 64.

Additional specimens of this species have not been examined so Turner's original description is given.

"♀. Mandibles shaped very much as in *striaticollis,* but more broadly flattened on the basal half and with a small tubercle near the base of the outer margin. Clypeus small, shining. Second joint of the flagellum about equal to the scape in length; the antennae inserted further from each other than from the eyes. Head opaque, a delicate longitudinal carina below the anterior ocellus. Pronotum much narrower than the head, longer than broad, the sides parallel, finely rugulose, the lateral margins raised, with a longitudinal median sulcus. Mesonotum and scutellum coarsely longitudinally rugose, the mesonotum with an impressed, obscure, longitudinal line on each side. Median segment narrowed to the apex and vertically truncate posteriorly, reticulated, the margins slightly raised and with three rather obscure carinae, the two lateral ones converging towards the apex. Abdomen smooth and shining. Second recurrent nervure received close to the base of the third cubital cell.

Black; mandibles and antennae, except the three apical joints, ferruginous; tegulae, tibiae beneath, and tarsi fusco-ferruginous. Anterior wings pale fusco-hyaline, a broad hyaline band crossing the first cubital cell. Length 6 mm.

Hab. Townsville, Q. (F. P. Dodd) November." (Turner).

This species seems to be most closely allied to *rufiventris* and *melanogaster.* There was no mention of the pubescence of the abdomen so one is led to believe that it is short and fine as in *melanogaster.*

Genus AUSTROTOMA, gen. nov.

Genotype *Aphelotoma aterrima* Turner, 1907, Ann. Mag. Nat. Hist. (7) **19**: 268.

Mandibles sickle-shaped, with an acute apex; in the female, clypeus clearly defined, more or less pointed at apex, which extends over the pointed labrum; antenna filiform, with funicle segments long, decreasing regularly in length; antennal sockets lying on the face, about as wide apart as each is from the eye. There is no median plate and the insertions of the antennae are slightly raised in the male. Pronotum large, without distinct protuberances; mesonotum divided longitudinally into 3 subequal areas by 2 deep sulci; lateral margin of propodeal declivity with a fine, acute projection, a finer one above at the posterolateral border; abdomen without distinct petiole; 4th tarsal segment not enlarged.

The genus shows affinity to both *Aphelotoma* and *Dolichurus*. It has a head somewhat like that of *Aphelotoma* and a propodeum and abdomen like those of *Dolichurus*.

AUSTROTOMA ATERRIMA (Turner)

Plate 1, Figs. 11 and 15

Aphelotoma aterrima Turner, 1907, Ann. Mag. Nat. Hist. (7) 19: 268.

Male

Head and thorax black, abdomen blackish but with faint reddish hues; antenna, tegula, and legs dark reddish black.

Abdomen shining, segments 2 and 3 with only scattered punctures, more so laterally, segment 4 more closely and finely punctate, particularly laterad and widely at posterior margin, segment 5 and succeeding segments glabrous anteriorly, finely punctate at posterior margin, increasingly so from meson to lateral margin.

Small species, length 5 mm; pronotum with a faint, median, longitudinal sulcus; face finely reticulate, tending to be vertically lined; with a small median projection above the level of the antennae; setae of face very short, face appearing bare; femoral furrow of fore leg with a small glabrous area behind, but most of furrow with ornamentation of rest of prothorax.

Female

Head and thorax black; abdomen blackish but with faint reddish hues; antenna red at scape, pedicel, and 1st funicle segment, darkening to apex; mandibles yellow except for extreme base and for the apical tooth; tegula and legs dark reddish black.

Abdomen shining at base, segments 2 and 3 with only scattered punctures and setae, more abundant and finer laterally on segment 3, segment 4 and succeeding segments densely clothed in short white setae except at meson of segment 4, there with scattered, larger punctures.

Small species, length 6.5 mm; pronotum with a shallow, median, longitudinal sulcus; face very finely pitted, with a small median projection above the level of the antennae; setae of face very short, face appearing bare; femoral furrow of fore leg semi-glabrous behind, ornamented in front.

Type.—Holotype ♂ in the British Museum.

Type locality.—Mackay, Qld.

Locality record.—QUEENSLAND: Kuranda (Oct. 1919, A. P. Dodd).

Genus DOLICHURUS Latreille

Dolichurus Latreille, 1809, Gen. Crust. Insect. 4: 387.

Genotype *Pompilus corniculus* Spinola, 1808 (monobasic and designation of Latreille 1810).

Mandible acute at the apex, with 2 small teeth just behind the apex in the female, and 1 tooth behind the apex in the male, in both an angular projection on the inner margin near the base; lateral sclerites of the clypeus not defined, completely fused with the median area; antennae inserted under a tegular protuberance which arises from the lower half of the face; all segments of the funicle very much longer than wide; pronotum large, as high as the mesonotum, which is divided longitudinally into 3 subequal parts by 2 deep sulci. The female usually has 4 macrochaetae on the clypeus, 2 rows of the same on the face, and a pair or more on the pronotum and scutellum. Scutellum large and flat, with a deep transverse groove just behind its anterior margin; lateral margins of the propodeal declivity furnished with a triangular tooth near or below the middle.

Only a single species of this genus is present in the fauna.

DOLICHURUS CARBONARIUS Smith

Plate 1, Figs. 9 and 12

Dolichurus carbonarius Smith, 1869, Trans. Ent. Soc. Lond. 1869: 303.
Dolichurus carbonarius Turner, 1915, Ann. Mag. Nat. Hist. (8) 15: 63.

Female

Body black, but apex of abdomen reddish; mandibles black, red at apical teeth; antenna, tegula, and legs dark reddish black, scape and bases of legs black.

Abdomen shining, glabrous, with a few punctures and setae laterally, more so on the posterior segments.

Medium-sized species, length 7 mm; face with irregular, vertical rugae, clypeus with truncate apex, surface with scattered, long setae, lower half of face finely setose; antenna with 1st segment of funicle as long as scape and pedicel combined; pronotum with distinct anterolateral and obtusely rounded posterodorsal projections, upper anterior margin strongly carinate, a faint median longitudinal sulcus over the anterior half, with a few distinct transverse rugae particularly over the anterior half; femoral furrow widely glabrous.

Type.—Holotype ♀. Location not known.

Type locality.—Australia.

Locality records.—QUEENSLAND: Dunk I. (Aug. 1927, H. Hacker); Brisbane (4.iii.1928).

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EXPLANATION OF PLATE 1

Fig. 1.—*Aphelotoma rufiventris* Turner, male from Bowen. × *c.* 4.
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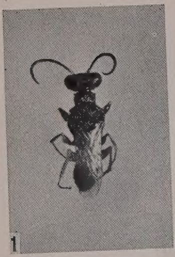
Fig. 13.—*Aphelotoma tasmanica* Westwood, enlarged view of male.
Fig. 14.—*Aphelotoma tasmanica* Westwood, enlarged view of female.
Fig. 15.—*Austrotoma aterrima* (Turner), enlarged view of propodeum.

AUSTRALIAN AMPULICIDAE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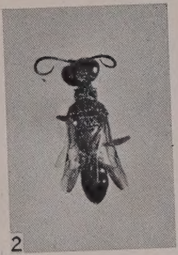
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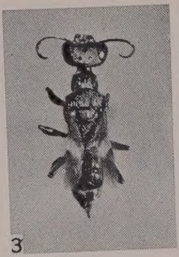
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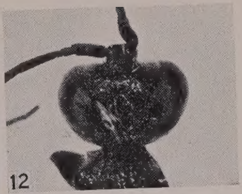
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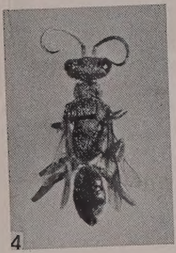
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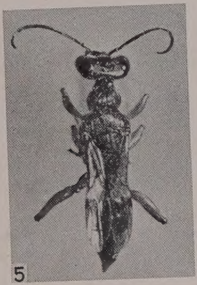
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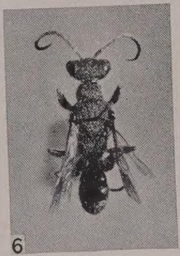
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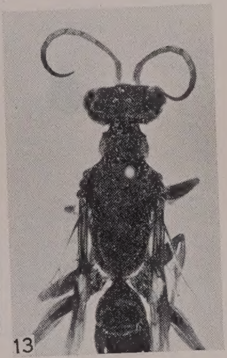
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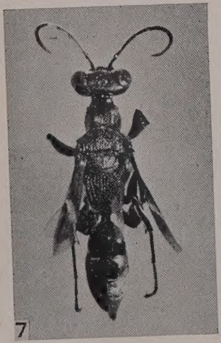
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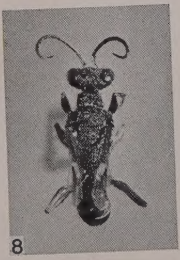
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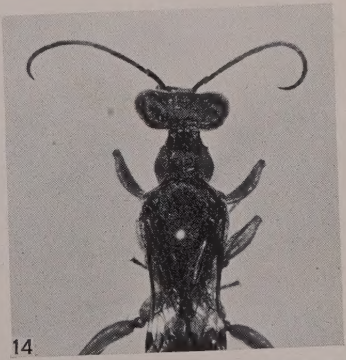
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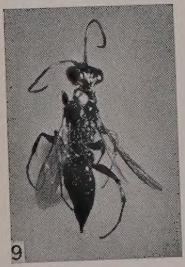
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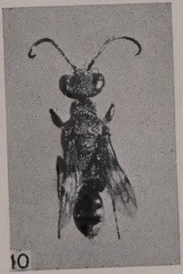
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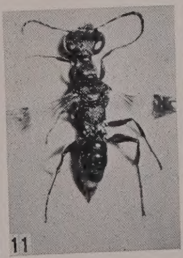
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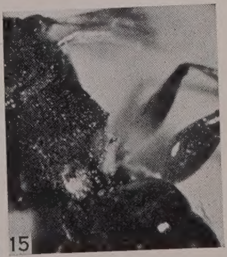
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